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STUDIES OF WOOD

I. THE CELL WALL¹

BY R. DARNLEY GIBBS²

Abstract

A brief review of literature relating to the nature of the cell wall is presented. The difficulty of separating lignin from cellulose is stressed, and attempts to effect separation by the use of mild solvents are described. The torus, pit membrane and border of bordered pits are more resistant to solution than the rest of the wall. The possibility of enzymatic analysis of the wall is noted.

General Introduction

In 1928 co-operation in work on the chemistry of the cell wall was requested by the Department of Cellulose Chemistry at McGill, and later, in 1929, inquiry was extended to the problem of sinkage of logs during the "drive" from woods to mill. The work would have been impossible without the following aids:

- a. Financial assistance from the Canadian Pulp and Paper Association through the Department of Cellulose Chemistry at McGill University, and from the Woodlands Section of the Association through its Forester, Mr. A. Koroleff.
- b. Grants to cover research and traveling expenditure from the National Research Council of Canada.
- c. The co-operation of Price Bros. and Co. Ltd. and of the Canada Paper Company in providing material, hospitality and assistance in the field.

The writer desires to express his gratitude to all of these. He extends it also to Professor Lloyd, in whose Department much of the work has been done, and to Professor Scarth who introduced the writer to the work and followed it with interest and very material aid; to Messrs. Jago and Walton of Price Bros.; to Dr. Hibbert of the Department of Cellulose Chemistry, and to Mr. Cleveland Morgan, who allowed use of his trees at Ste. Anne de Bellevue for experimental purposes.

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Contribution from the Department of Botany, McGill University, Montreal, Canada, with financial assistance from the National Research Council of Canada. From a thesis approved for the degree of Doctor of Philosophy in the University of London, England.

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This work falls naturally into three loosely related sections, of which the present paper constitutes the first. Later papers will deal with studies on the water content of certain (living) Canadian trees, on the changes in water content of logs during seasoning and flotation, and on the physiology of the tree with special reference to the ascent of sap and the movement of water before and after death.

The earliest cell walls, "middle lamellae", probably consist, as Mangin (38) suggested, very largely of pectic compounds. It is true that Tupper-Carey and Priestley (65) considered protein to be present in young walls of *Vicia faba* and *Phaseolus*, but Wood (67), using the "chloramine" reaction, claims that there are only extremely small amounts (0.001% or less) of protein in cellulose walls.

Recent work has widened our knowledge of the pectic compounds to a point where we may be fairly confident as to their chemistry though still somewhat confused as to their position and role in the cell wall. Among those who have contributed to this work we may mention Candlin and Schryver, Carre and Haynes, Conrad, Fellenberg, Nanji and Norman, Nanji, Paton and Ling, Norris, Norris and Schryver, and O'Dwyer. Much of their work is reviewed by Onslow (43). Apparently the materials in question are fairly easy of removal from the young cell wall by a variety of solvents and this results in a separation of the cells.

All the usual solvents for pectic compounds—boiling water, 0.5% oxalic acid, 0.5% ammonium oxalate before and after treatment with dilute hydrochloric acid—had very little effect upon microtome sections of spruce, pine, balsam, birch, lime, etc., which retained their strength and appearance even after prolonged treatment, so the middle lamella here can hardly be of pectic nature.

O'Dwyer (41, 42), however, has found small amounts of pectic materials in the woods of beech and oak, so it is evident that they are not entirely absent from lignified tissue. The idea of Candlin and Schryver (10), that a decarboxylation resulting in the formation of hemicelluloses may occur during lignification, might explain the apparent disappearance of pectins (see also (43), p. 86), but a change to hemicelluloses is quite insufficient to explain the behavior of the lignified wall, though the idea is of some interest in connection with the possibility that hemicelluloses are reserve foodstuffs. Chemical relation between pectin and lignin through hemicelluloses has been advanced as a possibility by O'Dwyer (42).

It has been shown by Ritter (51) that the mature woody wall behaves as if the middle lamella is composed of lignin rather than pectin. In his 1925 paper Ritter presented figures indicating that 75% of the lignin of wood is in the middle lamella, but Scarth, Gibbs and Spier (56) pointed out that this figure is impossibly high, the volume of middle lamella being far too small to account for so much lignin. Ritter himself appeared to think his results high and in a later paper (53) gave a lower figure. Harlow (19), in a brief review of the literature, quotes Haberlandt and Rhoads as recognizing that the middle lamella may be lignified, while Schellenberg (58) appears to have

noted this as long ago as 1896. Harlow sees two possibilities:—change of pectins into lignin, or the complete incrustation of pectins by lignin to render them insoluble. He ignores the possibility of the actual removal of pectins during lignification, or their transformation into hemicelluloses, as mentioned above. In a later paper (21) he described a method (chlorine water followed by hot 3% sodium sulphite) for the maceration of woody tissue, which is made possible by the lignin-like character of the middle lamella.

Let us turn now to a brief consideration of cellulose and its role in the cell wall.

A review by Schorger (59) of the theories as to chemical structure of cellulose appeared some eight years ago. In it Schorger compares the formulas of Haworth and Leitch (1919), Hibbert (1921), Irvine (1922-3), Karrer (1921) Karrer and Smirnov (1922), Hess (1923), etc. Most of these workers endeavored to explain the properties of cellulose by the postulation of ring structures composed of from two to four glucose or near-glucose units, but use of the polarizing microscope and the X-ray has resulted in the straight-chain* hypothesis. The papers of Herzog and Jancke (28), Sponsler (61-64), Clark (12), Preston (47), Zeidenfeld (68), Meyer (39) and Astbury, Marwick and Bernal (2) deal with various aspects of the subject.

The present position may be stated as follows: The almost theoretical yields of glucose in total, and the high yields of cellobiose in partial hydrolysis of cellulose lead to the suggestion that glucose in the form of cellobiose (β -glucosido-4-glucose) units forms the basal unit of the wall, while the results of optical (especially X-ray) analyses would appear to confirm this theory. The last has made it possible to calculate the space lattice in the wall, and the unit structure (longitudinal axis 5.15 \AA , radial spacing 5.33 \AA , tangential spacing 6.10 \AA (63)) that is indicated agrees very well with the conception of cellobiose aggregates. One of the greatest difficulties encountered in the X-ray work has been the selection of suitable material. Both Sponsler and Preston have found the wall of *Valonia* to be almost perfect material. Sponsler concluded that while the plane of "spacing" 5.33 \AA is perpendicular, or nearly so, and the plane 6.10 \AA roughly parallel to the wall, the cellulose-chain axis (5.15 \AA) is diffuse, the chains being arranged at various angles. Preston agreed with this finding, but Astbury, Marwick and Bernal (2), using single layers of wall instead of blocks of many layers as employed by Sponsler, have shown that there are ". . . two main sets of cellulose chains which form crystallites crossing at an angle which is maintained remarkably constant through the whole thickness and over considerable areas of wall." Further, these chains are parallel to the microscopically visible striae and their positions and relative numbers account for the behavior of the wall under polarized light.

Not only can the presence and orientation of chains be demonstrated but good evidence for the actual length of the chains may be obtained (1). It seems that *endless* chains would give 2, 3, 5-trimethyl glucose alone under carefully controlled methylation, while the *ends* of chains would give tetra-

*Each glucose residue is cyclic.

methyl glucose. Actually 0.6% of tetra-methyl glucose has been obtained and this would correspond to a length of 200-300 glucose units ($100-150\mu\mu$). The molecular weight of something over 30,000 calculated for this agrees well with X-ray, Svedburg ultra-centrifuge and Staudinger viscosity measurements, so we find all the evidence pointing in the same direction, even for such widely different structures as cotton fibres and tunicate mantles (39).

It is convenient at this point to consider the "micellar" character of the wall. Cellobiose chains of 200-300 glucose units would have a length of about $100-150\mu\mu$ and a thickness of about $0.5\mu\mu$, though the figures given by Seifriz (60) suggest a length of $60\mu\mu$ corresponding with a chain of fewer units. Meyer supposes that bundles of about sixty of the larger chains are combined with each other to a crystallite having lattice structure (the micellae) such as those of Seifriz (Fig. 1, C). The last considered that "The orientation of the crystallites is confined to the fact that the long axes are approximately parallel; aside from that, they may have any position or orientation and decidedly lack the regularity of bricks in a wall".

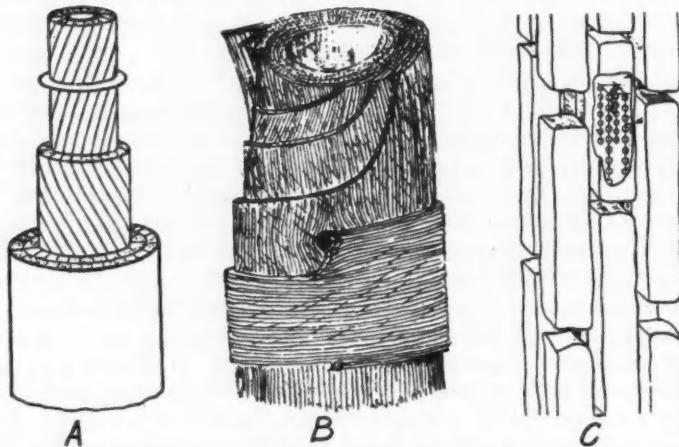


FIG. 1. *Structure of the cell wall. A. Cotton hair (after Meyer). B. Wood fibre (after Scarth in Scarth, Gibbs and Spier). C. Cellulose micellae (after Seifriz).*

The micellae referred to above, with a length of $100-150\mu\mu$ and width and thickness of the order of perhaps $5\mu\mu$, would not be visible even when swollen, but there is abundant evidence from microscopic work that the cell wall possesses a micellar or fibrillar structure which is visible under certain conditions (see Ritter (53), and Harlow (19)). This would seem to imply the aggregation of these smaller bundles into larger ones, as suggested by Herzog and Jancke (28). The long axis in all but the outer layers would run almost parallel to the fibre length, while in the outer layers the direction would be almost at right angles to this (see Fig. 1 and compare the behavior of fibres on swelling as described by Ludtke (36)).

In addition to longitudinal orientation there is a more or less transverse cleavage structure that is manifested in the "checks" often visible in fibre walls. These form a more or less definite angle (slightly less than 90°) with the longitudinal striae, and observation of their behavior during solution indicates that they run in definite series. These checks, taken in conjunction with the longitudinal cleavage planes, divide the wall into bricks that are probably much more regularly arranged than Seifriz appears to think. The formation of visible micellae, as we have seen, would render some such structure necessary.

The α , β and γ -forms of cellulose are considered to differ only in degree of dehydration or condensation, while oxy-cellulose differs from the normal in that it reduces Fehling's solution, has acid properties, and yields furfuraldehyde on distillation. This is understandable if the free $-\text{CH}_2\text{OH}$ group of cellobiose be oxidized to $-\text{CHO}$ and $-\text{COOH}$ groups (in different molecules, of course) and carbon dioxide split out of some of the latter to give xylose units (see de Chalmot (11) and Parsons (44)). Reports that celluloses from cotton and wood are different may perhaps be explained on similar grounds.

Lignin has always presented difficulties and it is idle to pretend that much is known even now as to its origin, structure and role in the cell wall. It cannot be referred, like cellulose, to relatively simple substances, nor can it be isolated with the complete confidence that it remains unchanged. Harlow (19, 21) points out that "lignin" of the botanist may not be the same thing as lignin of the chemist. It is customary for the former to regard walls as "lignified" when they give certain color reactions with such reagents as aniline sulphate, phloroglucin-hydrochloric acid, etc., while the latter classes as lignin material that is removable by chlorine-sulphite treatment or material left after removal of cellulose, etc. by acid. It has long been suspected that the color reactions are due to small amounts of substances of an aldehyde nature occurring with lignin but not necessarily a part of it (see Onslow (43), pp. 109-112). Klason (32) gives a formula for α -lignin of spruce which suggests that it is derived from two molecules of coniferyl aldehyde (which gives the phloroglucin reaction), but it cannot be claimed that this formula is definitely established. Harlow (22) has given much attention to the question of staining reactions of lignin and concludes that they are not altogether reliable, while Scarth, Gibbs and Spier (56) also investigated the correlation between staining and (chemists') lignin and found it to be close but not absolute. An extensive review of lignin chemistry is given in a recent paper by Phillips (45).

Attempts to correlate microscopical observation and chemical treatments of wood are of interest. Some of Ritter's observations have been quoted above. In other papers (50, 52, 53) he describes work which, in his opinion, indicates differences between hard- and soft-wood lignin, between amounts of lignin in heartwood and sapwood, and spring and summer wood (Ritter and Fleck (55)), and so forth. He describes "fusiform bodies" from lignin that may be identical with similar structures described by Kürschner (34) as formed

by fungus action on wood. Some of his results have been questioned by Harlow (19, 20, 21, 23, 24) who considers the "cell-wall lignin" of Ritter to consist of ". . . the charred decomposition products of the polysaccharides of the cell wall in addition to fragments removed from the lignin blocks by prolonged boiling". Harlow (23) notes, as did Scarth, Gibbs and Spier (56), and Ludtke (37), the different behaviors of the secondary walls of hardwoods and softwoods. He finds (24), however, that there is lignin in the secondary walls of hardwoods and that it may retain the form of the original cell after removal of cellulose. Although his chemical tests—complete solution as a result of several treatments with bromine followed by weak ammonia—would seem to indicate removal of all cellulose, it is difficult on viewing his photographs to convince oneself that such is really the case. Freudenberg, Zocher and Dürr (16), and Fischer and Lieske (15), however, also claim that lignin retains the shape of the cell wall after removal of carbohydrates, though considerable shrinkage may occur.

The usual solvents for lignin and cellulose are too drastic in their action, and workers are tending more and more to the use of milder solvents. Work is hampered by the lack of knowledge of the chemistry of lignin, and it is not even known for certain whether lignin and cellulose are in chemical combination. In this connection we may note that lignified walls are said to give the same X-ray picture as pure cellulose walls (17, 18). This would imply that lignin is between the micellae rather than part of them. The fact that color reactions for cellulose may not be given until after fracture of the lignified wall may also be in harmony with this view.

The use of milder solvents is to be commended on chemical grounds and is absolutely essential for microscopic work. In an effort to avoid the swelling and charring resulting from the use of 72% sulphuric acid, graded concentrations (on the principle used in cytology) were employed. This method had its advantages, and it proved possible to dissolve away all but the structurally unaltered (?) middle lamella from 15 μ sections. (Some lignin was, of course washed away rather than dissolved.) Even with very slow solution, however, there was considerable darkening and attention has therefore been given to milder solvents* in an effort to isolate the lignin or cellulose unchanged. Among the solvents used were:—

- (a) *For cellulose:* Sulphuric acid (all concentrations up to 72%); choral-pyridine; trichloracetic acid (at various concentrations in ether, water and dioxane solutions).
- (b) *For lignin:* Lactic acid; glycerol; glycol; aqueous glucose; chlorine in carbon tetrachloride, followed by ammonia; triethanol amine; methyl alcoholic sodium hydroxide (2%).
The first four were used alone, with 0.5% hydrochloric acid, with a trace of iodine, or with 0.5% hydrochloric acid and a trace of iodine. The

*Dr. H. Hibbert very kindly suggested and supplied some of the solvents tried. Mr. C. W. Argue also made a number of tests,—results unpublished.

last was employed in the cold, following the technique used by Beckmann, Liesche and Lehmann (5) on rye straw. The alcohol is said to prevent solution of hemicelluloses.

(c) *For pectic constituents:* $N/30$ HCl, followed by ammonium citrate as used by Conrad (13); ammonium oxalate; boiling water for long periods.

The technique employed varied greatly with the reagents. Some were used at room temperature only, others at controlled temperatures ranging from about 20–110° C. In a few cases, as when trichloracetic acid and triethanol-amine in ethereal solution were tested, the sections were sealed up in small vials and heated at 50–60° C. for various lengths of time.

The sections were obtained from *Alnus rubra*, *Tilia americana*, *Picea* spp., *Betula alba*, *Ochroma lagopus* (Balsa), and *Populus tremuloides*. Most of the solvents listed above were tried on all species, but the use of triethanol-amine and trichloracetic acid was confined for the most part to *Picea alba* and *Populus tremuloides*.

In almost all cases the sections proved very resistant to the solvents and retained their form and strength but little altered. Exceptions were: Sulphuric acid (not a mild solvent) and trichloracetic acid for cellulose, and lactic acid for lignin. Trichloracetic acid appeared to be fairly effective as a cellulose solvent but it was very difficult to be sure that all cellulose had been removed, even after treatments extending over several weeks. As representative of the type of result obtained, two experiments may be quoted.

1. Extraction of Lignin by Glycol

Sections were extracted with hot alcohol-benzene mixture, transferred to pure glycol, to glycol plus a trace of hydrochloric acid, or to glycol plus sufficient iodine to give a pale, straw-colored solution, and extracted at 110° C. for six to eight hours (Hibbert and Rowley (31), Hibbert and Marion (29), Hibbert and Phillips (30)). The solutions were then replaced, by slow stages, by water and the sections were mounted in phloroglucin-hydrochloric acid or in aniline sulphate-sulphuric acid. All gave "lignin" color reactions (red and yellow respectively) but somewhat less strongly than unextracted material, and all had retained their form and were still strong enough to handle. Gradual transfer to 72% sulphuric acid, to remove cellulose, did not result in complete solution, a network of material remaining which consisted largely of middle lamella. This residue (presumably lignin unextracted by the glycol) was subjected to treatment in cold 2% methyl alcoholic sodium hydroxide. After 48 hr. the network appeared to be but little changed.

According to Hibbert and his co-workers, glycol may extract up to 40% of the total cell wall material, but the actual "glycol lignin" recoverable is but a fraction of the total lignin. It is clear from our experiments that the middle lamella at least is but little affected either by the glycol or by the alcoholic sodium hydroxide.

2. Extraction of Lignin by Lactic Acid

According to Hibbert and Phillips, lactic acid containing 0.5 gm. hydrochloric acid per 100 gm. of wood meal extracts as much as 42% of the total material, while the lignin recoverable may amount to 14.1%*. This is a very large proportion of the total lignin and removal of this amount should have a profound effect on the microscopic appearance of wood.

In order to test this, spruce sections were extracted for about six hours at 110° C. with lactic acid-hydrochloric acid and marked maceration of the tissue was observed. The residue no longer gave the aniline sulphate or phloroglucin reactions, and on treatment with 72% sulphuric acid, almost complete solution occurred. There remained, however, *a thin lamella from the cells of the medullary rays and the pit-membranes, tori, and in some cases the arched "borders" of the pits* (Fig. 2).

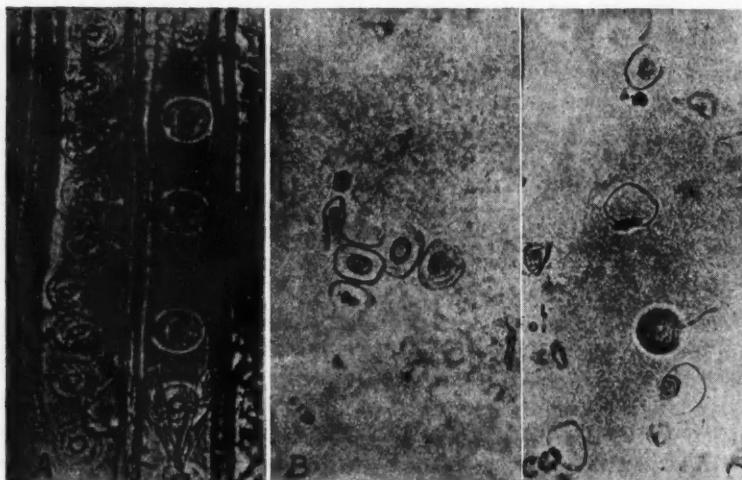


FIG. 2. A. Radial longitudinal section of spruce to show bordered pits. B. Isolated bordered pits (see text). Note torus at top left. Same magnification as A. C. The same. In three cases the tori are free from the borders which appear as colorless rings. Same magnification as A and B.

The isolated tori with the pit membranes reminded one strongly of the figures given by Bailey (3) and, in spite of the difficulty of observation, one could just distinguish in a few cases the pores (?) of the membranes as elongated radiating areas. Sometimes the membrane appeared to be dissolving from the edge and a rather regular raggedness, the indentations of which might correspond with the pores, was visible.

It is difficult to say to what this high resistance of torus, pit membrane and border is due, but the yellow appearance of torus and membrane and the complete lack of color of the border suggest that the two former are lignin

*Additional "soluble lignin" probably remains in solution.

and the last is cellulose. In sections treated under our conditions, residual lignin is yellowish and cellulose quite uncolored. The difficulties encountered by Scarth and Spier (57) when they tried to loosen the tori of red spruce heartwood are perhaps rendered more intelligible by these observations, while the high resistance of the medullary ray cells is in accord with the findings of Harlow and Wise (25), that in the rays of *Quercus alba* and *Casuarina inophloia*, which were chosen for the large size of their rays, the lignin is higher and the cellulose lower than in the wood as a whole.

The fact that lactic acid-hydrochloric acid mixture extracts 42% of the wall indicates that substances other than lignin are removed, and this is probably due to hydrolysis of hemicelluloses, etc. Lactic acid alone is not an effective solvent for lignin, and the necessary use of strongly acid mixtures rather removes it from the class of mild solvents. In fact, it is clear that none of the solvents tried is really specific for lignin and it is this that renders this type of work highly unsatisfactory.

Biological analysis of the cell wall. The employment of enzymes to bring about separation of the cell wall constituents has already received considerable attention at the hands of a number of workers.

R. Hartig (26) in 1878 published a volume on decay of woods, and Czapek (14) described as "hadromase" an enzyme capable of destroying lignin. Further investigations of the enzymes of fungi were made by Kohnstamm (33), Buller (8) and Reed (48). Much of this early work is reviewed by Potter (46), while papers by Zeller (69, 70) deal with the physiology of wood-destroying fungi and include fairly extensive bibliographies. From *Lenzites saeparia* Zeller described ligninase (the "hadromase" of Czapek), cellulase, hemicellulase, pectase and pectinase, as well as many other enzymes acting on simple sugars, etc. The fact that cellulose reactions are given by some woods only after attack by certain fungi has been advanced as proof that lignin and cellulose are combined in the cell wall (46), but we have already seen that X-ray data are against this idea.

While wood-destroying fungi are the most obvious sources of enzymes for this work, the macerating enzymes of fruits, the hemicellulases of the date, and the extremely potent cellulases of some animals might also be considered. There is the possible advantage that in using such material more specific reactions might be obtained, but it must also be remembered that some workers have claimed that cellulases may be so specific as to act only on celluloses from some sources (69, 70).

We may notice here a few of the more recent papers on this topic. Brown (7) studied the action of *Botrytis cinerea* on non-woody tissues and found that its activity results in maceration. This suggests that its action is practically confined to the middle lamella, which presumably was composed of pectic materials in the tissues studied. Bray and Andrews (6) followed the chemical changes in groundwood during decay. They found that the brown rots have a selective action on cellulose and record that in one case 54% of the cellulose

was hydrolyzed and only 3% of lignin. Barton-Wright and Boswell (4) came to similar conclusions as a result of a study of dry-rot (*Merulius lachrymans*) which hydrolyzed mannans and galactans, then cellulose, but not lignin. Campbell and Booth (9) remark that "decay of brown-rot type should be regarded as an acid hydrolysis", while Hawley, Fleck and Richards (27) state that though brown-rots (such as *Lenzites striata*, etc.) attack cellulose, the white-rots (*Polystictus hirsutus*, *Trametes pini*, etc.) preferentially destroy lignin. They found, however, that in the early stages *Polystictus* may also attack cellulose. Pentosans, apparently, were more readily used than hexosans, while Rege (49) also found that the pentosans are the most important. Certain thermophilous bacteria are destroyers of cellulose, and Viljoen, Fred and Peterson (66) describe a form that can hydrolyze cellulose rapidly at 65° C., at which temperature the action of lignin-destroying enzymes might perhaps be inhibited. In spite of all this work, however, enzymes have not yet been isolated in such a form that cellulose and lignin can be separately and quantitatively removed from woody tissue.

Apart altogether from the chemistry of the wall itself there is a further point which requires more thorough investigation and that is the transformation from sapwood to heartwood.

The permeabilities to water of heartwood and sapwood are widely different, the latter being many times more permeable than the former, and the difference usually is due either to pit closure (most softwoods) or to the formation of tyloses (hardwoods) in the cells of the heartwood, the changes being accompanied by the death of the living elements of the wood. We shall see in a later paper that the heartwood may have little or no free water in the cell lumina, while neighboring cells of the sapwood may be full of water.* No one as yet has explained adequately just how this drying may occur, though Scarth (personal communication) suggests that the water is removed by tension from above after the area to become heartwood has been cut off from supplies from below. We have already noted the resistance to solution of the bordered pits and the difficulties encountered by Scarth and Spier in their attempts to open pits, and we must admit that the nature of the material causing pit closure has not so far been established.

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*Death of diseased trees may be due to the premature formation of "heartwood" through abnormal tylose formation (35), or to closure of pits (Nelson and Beal (40) and private note to Scarth). In both cases water is unable to pass the abnormal areas.

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STUDIES OF WOOD

II. ON THE WATER CONTENT OF CERTAIN CANADIAN TREES AND ON CHANGES IN THE WATER-GAS SYSTEM DURING SEASONING AND FLOTATION¹

BY R. DARNLEY GIBBS²

Abstract

The chief species studied were paper birch, poplar (*Populus tremuloides*), jack pine, white spruce, and balsam fir.

Methods for the study of water contents are described. Determinations of densities and swelling percentages are summarized. Conversion factors that may be employed to convert moisture contents based on dry weight into percentages of original volume are:—for jack pine 0.38, for balsam 0.315, for poplar 0.42 and for birch 0.49.

The hardwoods examined show a maximum water content in spring and a sharp drop in the summer. This appears to vary from year to year and the possible reasons for this variation are discussed. In 1931 birch and poplar lost half their total (spring) water during the summer months. In birch this may not be made up until the following spring. The softwoods show no marked seasonal changes in water content.

The distribution of water is characteristic for each species. Changes in distribution throughout the year have been followed. In birch all parts of the wood (there is no heartwood) join in the seasonal changes; in poplar only the sapwood varies in water content. The results of individual year-ring analyses and of borings at different heights point to uniform water content in corresponding parts of the tree.

Diurnal changes in water content have been investigated and rapid fluctuations recorded. These point to a decrease during the morning followed by an increase later in the day. These variations are correlated with tension changes and no doubt also with transpiration. It seems certain that the actual amount of gas in the tree varies but little during the diurnal changes, though it does vary with the seasonal fluctuations in water content.

Girdling of birch, balsam and spruce is described and the effects on water contents are followed. It is shown that in the case of birch, removal of wood to a depth of more than one inch leads to little change during two seasons. This is correlated with the continued activity of all parts of the wood. In balsam, almost complete drying of the sapwood within two or three months follows girdling through the sapwood. The characteristic wet patches of balsam heartwood, however, are unaffected, and it is concluded that these have no connection with the sapwood and so play no part in water conduction. The results from spruce are irregular.

Experiments on seasoning and flotation in the field and in the laboratory are described. The summer seasoning of "sour-felled" birch is more rapid than that of normal or of peeled logs or the normal water loss of living standing trees, and this must be due to evaporation from the leaves.

The effects of log length, of barking, and of end and/or side painting on rate of penetration of water have been investigated. While penetration of water is chiefly through the ends of logs, escape of dissolved air is largely in the radial direction, and so end penetration is less important than might be expected. There is considerable top drying from unseasoned floating logs (in laboratory tanks), which may assist in solution and removal of air and so hasten rather than slow up sinkage of the log. Seasoning followed by end-painting results in very slow entry of water and so is excellent in flotation.

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Introduction

This is the second of a series of three papers under the general title of "Studies of Wood". The first (12) dealt with work on the structure of the cell wall. The present paper approaches the subject from an entirely different viewpoint.

The density of actual wood substance is about 1.52-1.56. It is therefore denser than water and wood floats only because of entrapped air. It is well known that the natural gas content of wood varies with the species considered and with the season.

In eastern Canada, logs are floated from wood to mill, and when gas content is low, or when the "drive" is long, buoyancy may be lost and the logs sink. The following studies were carried out with a view to determining (a) the season at which trees are driest, and (b) the changes in water content caused by girdling, by seasoning, and by flotation. The hardwoods—birch and poplar—are notoriously poor floaters, so that attention has been concentrated on these. At present they are often left standing because flotation is so uncertain.

Acknowledgment of help received in this work has been made in the first paper of the series.

The following trees were studied:—

paper birch (*Betula alba* var. *papyrifera* (Marsh) Spach.), poplar (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb), white spruce (*Picea canadensis* (Mill.) P.S.P.), balsam fir (*Abies balsamea* (L) Mill.);

and to a lesser extent:—

sugar maple (*Acer saccharum* Marsh), tamarack (*Larix laricina* (DuRoi) Koch), yellow birch (*Betula lutea* Michx. f.).

In earlier work it was decided that for certain purposes the selection of groups of three trees, and the averaging of results from each group, gave sufficiently trustworthy results. From each tree, sets of samples out of top, middle and butt logs were taken, the nine sets of samples so obtained being referred to as "standard lots". "Butt" samples were taken about three feet from the ground, "middle" samples from the unbranched trunk at about 25 ft., and "top" samples at 40-50 ft., in the crown of the tree. For the most part, two discs were taken from each region, one being used as a whole, the other being chipped into smaller sections, very much as was Craib's (6, 7, 8) material. Two objections to these methods have been advanced. In the first place, they involve destroying the tree, which limits its use to a single experiment; second, there is a possibility (if high tension exists in the tree) of marked changes in water distribution during cutting. Objections have been met as follows:—

a. A borer on the lines of the common "increment" borer, but giving cylinders of wood $\frac{1}{8}$ in. in diameter, was used for several series of experiments.

b. Punchings were made, with a hollow punch giving a cylinder $\frac{1}{2}$ in. in diameter. This was placed against the tree after removal of the outer bark and driven home by a single smart blow from a heavy hammer. There was no chance in this case for migration of water on release of tension, except in a radial direction, and this could not occur in the second or two elapsing before removal of the punching. This method could be used only for the outer half-inch or so of the wood, but it is in that region that higher tensions and possible migrations are to be expected.

The results from a series of experiments carried out on a hot dry day, when tensions were high, were so nearly uniform that it was concluded that any or all of these methods might be employed with reasonable confidence.

It is well, perhaps, to explain more fully the exact technique involved in these methods. Craib (6, 7, 8) and Robert Hartig (15, 16, 17) employed the disc method, the former in his later work taking four strips from outside to centre. Birch, jack pine and spruce have been found so regular in their water distribution, however, that a single transverse strip divided into nine pieces (1 and 9, 2 and 8, 3 and 7, and 4 and 6 being averaged) has been used. In all but the birch the samples were of such a size that 1, 2 and 3, and 7, 8 and 9 represent sapwood, the others being heartwood. Poplar and balsam have much more irregular water content, but the errors due to the strip method as against division of the whole disc are comparatively small. The blocks, as removed from the strip, are rapidly trimmed on all sides (to eliminate errors due to surface drying) and weighed at once in the field. Borings and punchings are placed at once in weighed rubber-stoppered bottles and weighed at leisure. In all cases the first weighing is recorded as "wet weight"; the samples are dried for 36-48 hr. at 100 to 105° C. in an electric oven, cooled in a desiccator and weighed as rapidly as possible for "dry weight".

Distribution of Wood, Water and Gas in the Tree

The walls of wood in the natural state are saturated with water, since *free* water is always present somewhere in the tree and the imbibition pressure of the cell wall is very high. Several authors—Robert Hartig (15-17), Dunlap (9), Pidgeon (24), Grace and Maass (14), Wilson (36), Sachs (26)—have attempted to determine this water.*

It is doubtful whether the true values for the water held by the wood itself can be determined, as condensation takes place in the lumina of the cells, but by extrapolation of adsorption and desorption curves, Pidgeon and Grace and Maass obtain comparative values which probably approach them very closely. These authors give a higher value for pine than for spruce, while Robert Hartig, using different species, found the value for pine consider-

* Since writing the above our attention has been called to the work of Beversluis (*Mededeel. Landbouwhoogeschool Wageningen* 35 : 3-31, 1931. English summary). As a result of shrinkage studies he concludes that ". . . fibre saturation-point, therefore, does not correspond with a moisture content of the wood of 25-30%, as is generally stated, but with one of 15-16% (of oven-dry weight)".

ably lower than that for spruce (Table I). Barkas (1), using an optical method for the determination of adsorption of water by wood, records a value of 20% for adsorption on Sitka spruce flour, indicating that non-capillary forces hold most of the water of saturation.

TABLE I
SATURATION VALUES AND NATURAL WATER CONTENTS OF CERTAIN WOODS
(Values expressed as % based on dry weight)

Species	Saturation value, etc.	Natural water content (average throughout the year)
<i>Pinus sylvestris</i>	Hartig 30 (heartwood) Sachs 31 Pidgeon 31 (sapwood—absorption)	Hartig 31 (heartwood) Gibbs 33 (heartwood)
<i>Picea excelsa</i> <i>P. canadensis</i>	Hartig 37 (heartwood) Grace and Maass 28 (heartwood— desorption) Pidgeon 24 (sapwood— absorption)	Hartig 37 (heartwood) Gibbs 40 (heartwood)
<i>Betula verrucosa</i> <i>B. papyrifera</i> <i>B. lutea</i>	Hartig 42 (heartwood ?) Grace and Maass 27 (desorption ?) Wilson 27 (used two differ- ent methods) 29	
Average of seven American species	Dunlap 33 (about)	

In the standing tree, while free water is always present in the sapwood, there may or may not be free water in the heartwood. The remarkably constant figures obtained for water in jack pine and spruce heartwoods suggest that in these cases no free water is present. Robert Hartig thought this to be the case (Table I). The values given for natural water content of heartwood are averages of large numbers of determinations and include results from samples which, without doubt, had a little free water, so they are probably slightly higher than the true values for wall saturation.

The free water which is usually present in the cell cavities of the sapwood is rarely sufficient to fill all the lumina, the remaining spaces containing a gas mixture of variable composition. Thus, in order to have a clear conception of wood, it is necessary to know the volume and density of wall material, the volume of water, the volume and nature of the gas, the distribution of wood, water and gas in the sample, how this last changes in the living tree, and how, and at what rate, it can be changed by seasoning and flotation. The necessary procedure has been described in earlier papers (11, 13) and need not be detailed here.

If measurements of appropriate series of blocks be made, the variation in gross composition throughout the tree at various seasons may be determined. The distribution of wall substance will not vary from season to season and, when once investigated, may be taken for granted, so that from measure-

ment of water content we may obtain the gas content by difference (i.e., $\text{gas} = 100 - (\text{wood} + \text{water})$). In practice it is found that the percentage of space occupied by cell wall in a block of wood varies but slightly for a given

TABLE II
AMOUNT OF CELL WALL, DENSITY AND SWELLING OF CERTAIN WOODS

Species	Position in tree	% wood (based on fresh vol.)	Density (water = 1.0)	Swelling (% of dry vol.)	Remarks
<i>Pinus banksiana</i>	Centre of heartwood	23—	0.39	8	Average of four logs
	Outer sapwood	25+	0.45	12	
<i>Abies balsamea</i>	Sapwood:— outer	19	0.34	11	Average of top, middle and butt logs from each of three trees. (See also Fig. 1).
	mid.	19	0.34	12	
	inner	20	0.35	12	
	Heartwood:— outer	20	0.35	10	
	centre	22	0.38	9	
<i>Betula papyrifera</i>		Average 33. Usually lowest at centre, highest at outside. Usually higher in slowly grown logs	Average 0.6. Usually denser toward outside of log. Higher in slowly grown logs	17 to 24 Average 21	Average of 14 logs. (See Gibbs (11, p. 432) and Fig. 5). Results variable; not correlated with position
<i>Populus tremuloides</i>		Average 27. (20–25 in a log with 6 rings to the inch; 27–30 in a log with 19 rings to the inch)	Ranged from 0.37 to 0.55. Average 0.47	12	Average of 4 logs. Results very variable

species and may be taken as constant for all but finer work. The slight variations found are perfectly definite, however, and to a certain extent characteristic for some trees. The results of the present studies and of those of R. Hartig (15–17) are summarized in Table II and in Figs. 1, 2 and 3.

Reference to Hartig's results (Figs. 2 and 3) show that while the sapwoods of

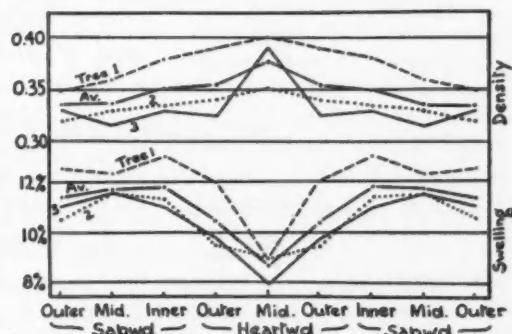


FIG. 1. *Abies balsamea*. Density and swelling. Each curve represents average of top, middle and butt logs.

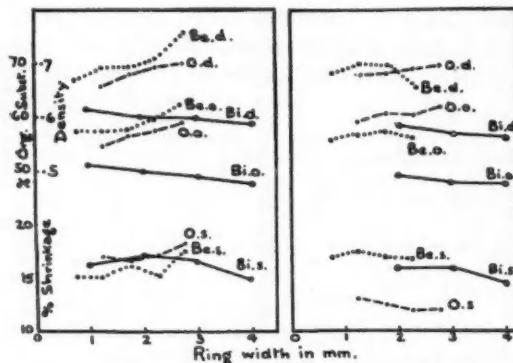


FIG. 2. Density, wall substance and shrinkage of certain woods as related to ring width (from R. Hartig's figures). Hardwoods (sapwood left, heartwood right): d = density (water = 1). o = organic substance (gm. in 100 cc. fresh wood). s = shrinkage (% of fresh volume). Be = beech (*Fagus sylvatica*). Bi = birch (*Betula verrucosa*). O = oak (*Quercus pedunculata*).

wish to calculate the proportions of water, "wood" and gas in a given sample. If we take average figures for density, "wood" and swelling for each species and apply these to any particular sample, the error involved is considerable but calculations of water, "wood" and gas from the easily obtained wet and dry weights of a piece of wood are sufficiently accurate for comparative purposes. The "conversion factor" for converting "% water based on dry weight" into "% water based on original fresh volume" is

larch, oak and beech showed increasing density, organic substance (the equivalent of "wood" in Table II) and swelling with increasing ring width, the remaining woods examined all showed exactly the reverse relations. These differences are probably due to variations in the relative proportions of spring and summer woods in the tree (4). Where wide rings are due to continued formation of summer wood, density should increase with ring width, and vice versa. The variations observed are of some importance when we

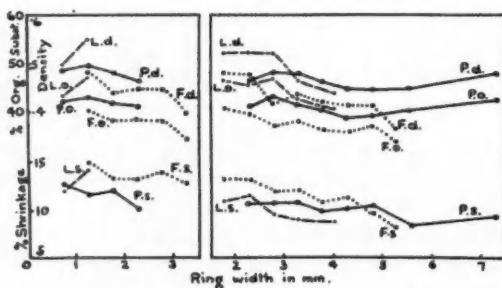


FIG. 3. Density, wall substance and shrinkage of certain woods as related to ring width (from R. Hartig's figures). Softwoods: L = larch (*Larix europaea*). P = pine (*Pinus sylvestris*). F = fir (*Picea excelsa*).

$$\frac{\text{density} \times \text{dry volume}}{\text{wet volume}}$$

(see Gibbs (11)). These factors for the trees examined work out at 0.38 for jack pine, 0.315 for balsam, 0.42 for poplar, and 0.49 for birch.

Seasonal Changes in Water Content

The trees used came from three stations:—

- near Lac Onatchiway, about forty miles north of Chicoutimi,
- near Ste. Anne de Bellevue, twenty miles from Montreal, and
- from Windsor Mills, P.Q. (yellow birch only).

As the first station is three hundred miles from Montreal, earlier material was sent in by express and the consequent delay in handling led to errors which were evaluated by a series of tests; birch, spruce and poplar logs being sampled in the bush and as received at the laboratory at Montreal. The changes in the water content of spruce and birch were found to be slight, that in poplar was somewhat greater. All later work was carried out in the field.

1. PAPER BIRCH (*Betula alba* VAR. *papyrifera*)

(a) Strip and Disc Method. *Lac Onatchiway* Material (Table III)

The water content of the tree as a whole fluctuates during the year, the maximum occurring just before leaf opening (end of May), the minimum in July and August (Fig. 4). In 1930 the minimum was just over 80% (based on dry weight). In 1929 it was probably lower than that (though higher, for the reason stated, than the figure indicated, 54%), while in 1931 it was 54%. This value was recorded in July and again in August.

It is quite possible that the maximum has been missed, for calculations from volume and density measurements indicate that the wood of the trees investigated could hold at saturation about 135% of water. This would correspond to a density of 1.16 and gas content of 0%. In wood with red heart, figures in excess of 130% (i.e., about the possible maximum) have been noted, but the highest water content of a tree, as a whole, that has been encountered was 103% in early June, 1930. This corresponds to a density of 1.00 and gas content of about 22% of the volume. Merwin and Lyon (23) have reported figures suggesting approximation to saturation during sap flow. It might be thought that the water content of the tree during the period when sap flows would remain more or less constant, but a fall in water content of standing trees at a time when stumps of cut trees continue to bleed has been noted.

It is, of course, no mere coincidence that the maximum water content is just before leaf opening and the minimum just before leaf fall, but this point will be discussed in detail in the third paper of this series.

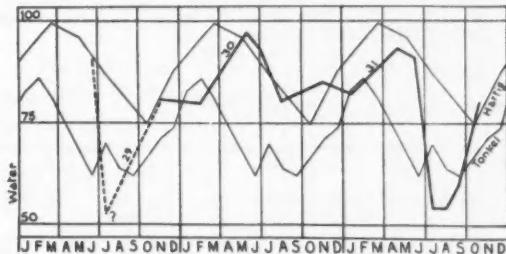


FIG. 4. Birch. Change in water content of whole tree throughout the years 1929 to 1931. The results of Hartig (15, 16) and Tonkel (quoted in 4) are included. They represent results for a single year, but are repeated for purposes of comparison.

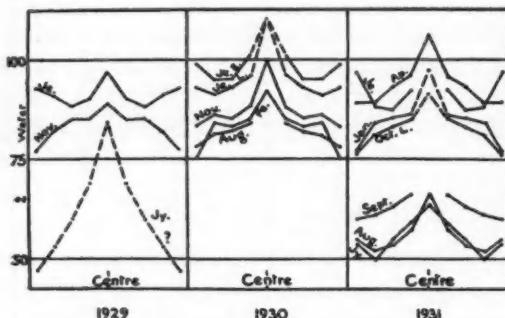


FIG. 5. *Birch. Changes in distribution of water across tree during years 1929 to 1931. Most curves represent averages of nine logs from three trees (Table III). Je. E.—early June. Je. L.—late June. Oct. L.—late Oct. Curves are dotted where unreliable owing to presence of red heart or other causes (see text)*

So far, only the total amount of water in the trees has been considered; there remains the question of lateral and longitudinal distribution. This is indicated by Fig. 5, and Table III. It will be seen that, while the top logs are usually a little drier than the butt logs, the differences are slight and somewhat irregular (see below for further comment on this point).

TABLE III
SEASONAL CHANGES IN WATER CONTENT OF BIRCH
(Disc and strip method)

Date	Remarks	Position in tree	Water (as % dry weight)						Water in disc (calc.)
			Outside to centre						
1929									
June	Samples analyzed in lab.	Average	93	91	88	90	97	—	91
July	Samples analyzed in lab. Some delay. Ten trees.	Average	47	53	60	69	84	—	54
Nov.	Considerable delay in sampling. Four trees.	Average	77	82	85	85	89	—	81
1930									
Feb.	Sampled at lab. Short delay. Three trees.	Tops	66	82	82	83	89	—	76
		Middles	78	89	84	85	95	—	83
		Butts	80	82	84	86	—	—	82
		Average	75	84	84	88	(92)	—	80
Early June	Sampled at lab. Wrapped for shipment. Three trees.	Tops	97	96	97	97	100	—	97
		Middles	95	93	93	97	101	—	94
		Butts	105	95	95	108	130	—	100
		Average	99	95	95	101	(110)	—	97
June 24	Sampled when felled. Three trees.	Average	93	91	93	96	(110)	—	93
Aug.	Sampled at lab. Wrapped for shipment. Three trees.	Average	78	81	82	85	90	—	80
Oct.	Sampled in bush. One tree.	Average	91	82	80	81	88	—	85

TABLE III—Concluded

SEASONAL CHANGES IN WATER CONTENT OF BIRCH
(Disc and strip method)

Date	Remarks	Position in tree	Water (as % dry weight)					Water in disc (calc.)
			Outside to centre					
1930								
Nov.	Samples wrapped for shipment. Three trees.	Tops Middles Butts Average	81 83 86 83	89 85 83 86	89 83 83 85	91 88 86 88	94 103 — (98)	86 84 85 85
1931								
Jan.	Sampled in bush. Three trees.	Tops Middles Butts Average	71 79 82 77	82 86 84 84	85 87 83 85	87 88 84 86	88 97 108 (97)	79 84 83 82
Late April	Sampled in bush. Three trees.	Tops Middles Butts Average	59 103 105 89	81 93 91 88	98 94 85 92	102 96 93 97	106 111 108 108	78 98 96 91
Early June	Sampled in bush. Three trees.	Tops Middles Butts Average	80 107 105 97	80 93 94 89	80 90 90 87	83 93 99 92	93 104 128 (108)	80 98 98 92
July	Sampled in bush. Three trees.	Tops Middles Butts Average	58 52 53 54	50 48 52 50	53 53 55 54	57 58 62 59	63 68 62 64	57 52 54 54
Aug.	Sampled in bush. Three trees.	Tops Middles Butts Average	59 52 55 55	55 51 51 52	56 54 52 54	58 58 58 58	66 64 67 66	57 53 54 54
Sept.	Sampled in bush. Three trees.	Tops Middles Butts Average	54 57 69 60	55 59 70 61	57 60 72 63	57 63 77 66	67 72 82 (74)	55 59 71 62
Late Oct.	Sampled in bush. Three trees.	Tops Middles Butts Average	70 83 78 77	83 84 85 81	87 85 86 83	86 (91) (93) (91)	89 84 83 85	79 84 78 80

Figures in bold face include red heart. Averages bracketed are incomplete.

There is no indication of heartwood and sapwood in paper birch but the greater variations in water content of the younger wood seem to indicate that it serves more effectively as a water channel than do the inner parts of the tree. Scarth (unpublished work), using similar trees, found that dyes on entering borings rose more rapidly in the outer rings.

The work of MacDougal, Overton and Smith (22) on distribution of gas in the tree suggested an examination for variations from ring to ring. Quantitative determinations of water content in a single ring proved difficult but not impossible. Results are drawn from the following material:—

October, 1930.

Birch—Top, middle and butt logs from a single tree.

Poplar and spruce—Top, middle and butt logs from each of three trees.

January, 1931.

Birch, poplar, balsam and larch—Top, middle and butt logs from each of three trees.

Spruce—Top, middle and butt logs from each of two trees.

July, 1931.

Birch, poplar and spruce—Top, middle and butt logs from each of three trees.

Balsam—Top, middle and butt logs from each of two trees.

The complete series is summarized in Fig. 6, the curves representing averages of samples from top, middle and butt logs.

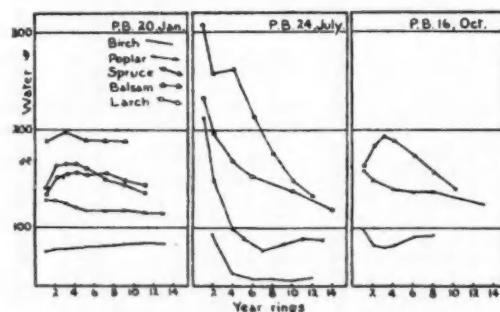


FIG. 6. Water content of outer rings at different seasons. The water content is expressed as percentage of dry weight. The numbering of rings is from the outside.

The change in form of the curve for water content is really less striking than appears from Fig. 6, for it must be remembered that Ring 1 of the July samples is the newly formed ring, absent from those of January. It has a very high water content in spruce, poplar and balsam, and no doubt in birch also, but in the last it was not possible to separate it from the other rings.

The changes in the other rings are not great, but there are indications of some seasonal changes in the softwoods. This is of interest since gross analyses do not bring these out (see below). Those of poplar and birch show decreased water content in July, corresponding to the general decrease in the tree as a whole. The ring for the current year contains less water in October than in July, which is to be expected.

(b) *Boring Method. Lac Onatchiway and Ste. Anne's Material*

Results are summarized in Fig. 7. The fall in water content as indicated by figures from cut trees is demonstrated even more effectively here. It is interesting to note that the smaller birch at Ste. Anne's shows a fall to a lower value than the larger trees near Lac Onatchiway. The much later leaf opening and earlier leaf fall at the latter station (which is further north and at an elevation of about 1,000 ft.) also are reflected in the figures. When borings were taken in October 1931 at Lac Onatchiway bleeding was noted. This is rather unusual at that season, but was somewhat less surprising in view of the spring-like weather which prevailed at the time.*

2. *YELLOW BIRCH (Betula lutea)*

A few figures from *Betula lutea* indicate a comparable drop in water content during the summer months. Two large trees (ca. 18 in. D.B.H.) at Windsor Mills, P.Q., were bored to a depth of one inch on June 3, 1932. The moisture contents of the borings were 94 and 84% respectively, while in early September they were 61 and 50%.

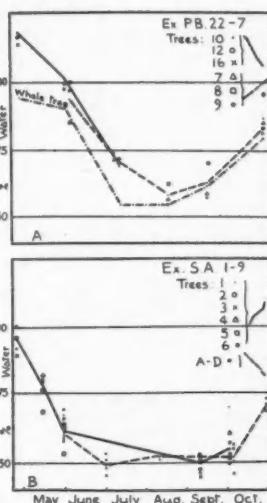


FIG. 7. *Birch. Decrease in water content during the summer of 1931, as shown by borings to a depth of one inch.*

A. On the Price Brothers Limits, two sets of trees D.B.H. 8 in. The water content of whole trees, as determined by the disc method, is added for comparison.

B. Near Ste. Anne de Bellevue, two sets of trees D.B.H. 4 to 5 in.

3. *POPLAR (Populus tremuloides)*(a) *Strip and Disc Method. Lac Onatchiway Material. (Figs. 8 and 9, and Table IV.)*

TABLE IV
SEASONAL CHANGES IN WATER CONTENT OF POPLAR

Date	Remarks	Position in tree	Water (as % dry weight)						Water in disc (calc.)	
			Sapwood			Heartwood				
			Outer	Mid.	Inner	Outer	Centre			
1930										
Early Feb.	Sampled at lab. Short delay. Three trees.	Tops	147	125	100	65	60	123		
		Middles	156	123	93	55	62	123		
		Butts	162	130	102	74	78	132		
		Average	155	126	98	65	67	126		

* Dr. C. W. Townsend on October 6, 1927, found sap flowing from fresh holes made by a yellow-bellied sapsucker in an apple tree (personal note to Professor V. C. Wynne-Edwards). Autumnal bleeding is probably more common than is usually supposed.

TABLE IV—*Concluded*
SEASONAL CHANGES IN WATER CONTENT OF POPLAR

Date	Remarks	Position in tree	Water (as % dry weight)					Water in disc (calc.)	
			Sapwood			Heartwood			
			Outer	Mid.	Inner	Outer	Centre		
1930									
Late April	Sampled at lab. Short delay. Three trees.	Tops Middles Butts Average	116 131 131 126	106 111 127 115	89 93 128 103	79 72 72 74	75 62 56 64	104 112 123 113	
Mid-Aug.	Sampled at lab. Short delay. Three trees.	Tops Middles Butts Average	100 84 78 87	94 83 75 84	78 77 92 82	70 69 97 (79)	79 67 112 (89)	91 81 82 84	
Late Oct.	Sampled in bush. Three trees.	Tops Middles Butts Average	132 154 125 137	115 132 96 114	84 105 81 90	79 80 71 77	66 77 74 72	112 130 102 115	
Mid-Dec.	Sampled at lab. Very short delay. Three trees.	Tops Middles Butts Average	151 160 156 156	128 135 146 136	108 106 136 117	91 59 97 (82)	53 61 65 60	130 132 143 135	
1931									
Jan.	Standard lot of three trees. Sampled in bush.	Tops Middles Butts Average	134 123 115 124	122 114 104 113	104 104 101 103	69 60 73 67	63 64 96 (74)	118 110 105 111	
Late April	Standard lot of three trees. Sampled in bush.	Tops Middles Butts Average	136 143 163 147	118 126 128 124	101 108 100 103	54 73 107 (78)	54 70 116 (80)	115 124 134 124	
June	Standard lot of three trees. Sampled in bush.	Tops Middles Butts Average	105 88 86 93	99 78 76 84	88 80 81 83	60 62 111 (78)	68 69 122 (86)	95 80 85 87	
Aug.	Standard lot of three trees. Sampled in bush.	Tops Middles Butts Average	96 79 83 86	87 76 73 79	81 78 72 77	62 57 92 (70)	57 49 81 (63)	87 76 79 81	
Sept.	Standard lot of three trees. Sampled in bush.	Tops Middles Butts Average	80 67 61 69	76 66 60 67	70 66 63 66	61 66 — (64)	57 64 — (61)	75 66 61 68	
Late Oct.	Standard lot of three trees. Sampled in bush.	Tops Middles Butts Average	131 105 92 109	116 92 93 100	96 57 106 98	(46) — 91 (65)	59 62 78 (66)	111 94 95 100	

Figures in bold face are from blocks with rot; figures bracketed are averages including such values or are from incomplete records.

The water content of the tree as a whole varies very much as does that of birch, a decided drop in water content occurring during the summer months. Certain differences, however, are apparent. The percentage of water present is decidedly higher, ranging from about 130 in December to 65 in September (the maxima and minima for birch are about 100 and 50), and the maximum water content may be in December rather than at leaf opening. Poplar is more variable than birch and one must be conservative in estimates of the reliability of figures. Thus, in December 1930, a water content of 129% was recorded, as against 109% and 117% in January and April, 1931. It is possible that this lower value in January *really* records loss of water from the bark during the time when the soil is frozen and root activity (presumably) is completely at a standstill, and the higher figure for April may correspond to the sap-flow maximum of birch. Poplar logs lose water much more rapidly than birch or spruce, and the loss by evaporation from the leafless tree may also be relatively great. Experimental evidence for this is given in a later paper. Tonkel (see Fig. 8), working in Russia, though finding a continued rise from September to February, recorded a slight fall as early as March—some time before root activity could have commenced in such a rigorous climate.

The very different summer values obtained for birch in 1930 and 1931 are again met with here. The lowest figure recorded for poplar in 1930 was 86 (in August), and even this was lower than the actual value owing to loss in transit, while the results for June, August and September of 1931 are about 85, 80 and 65 respectively. The September figure for poplar is considerably below the August value: in birch the water content is rising by September. This is correlated with the fact that birch was losing its leaves during the latter month, while those of poplar remained quite green and functional. In both species, however, there is a marked upswing in October, following complete defoliation.

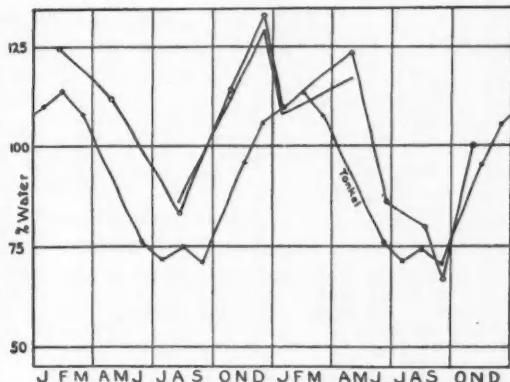


FIG. 8. Poplar. Changes in water content of whole tree throughout the year. The line with crosses is from Tonkel (in Büsgen (4)). The line with dots joins values obtained from discs; the line with circles, values obtained by calculation from those of small blocks. Tonkel's curve is repeated for comparison. The other curves are from records for February 1930 to October 1931 (Table IV).

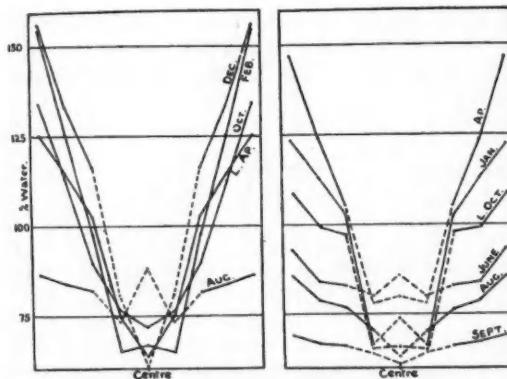


FIG. 9. *Poplar. Changes in distribution of water across the tree during 1930 (left) and January–October 1931. Curves are dotted where unreliable owing to presence of fungus infection.*

The sapwood throughout the winter is very wet. The maximum possible water content of poplar is about 170% (based on dry weight) and in December and February of 1930 over 150% of water in the outer sapwood (after some loss during transit) was recorded. As one passes inward a steady decrease in water is noted, but the value rarely falls below 100% in the winter months. Throughout the summer a very marked decrease in water content of sapwood occurs and this was particularly marked in 1931, dropping to about half the winter value. For water contents of individual rings see Fig. 6.

(b) *Boring Method (Lac Onatchiway and Ste. Anne's Material)*

Results are summarized in Fig. 10.

4. *JACK PINE (Pinus banksiana)*

The results from jack pine are so uniform as to need very little discussion here. The heartwood seems never to contain free water. The water present, which is sufficient only to saturate the cell walls, averages about 34%. The sapwood is always wet and there is no evidence of

Distribution in the tree is very different from that of birch (compare Figs. 5 and 9). This, of course, is due to the formation of heartwood in poplar. The heartwood occupies only a relatively small proportion of the volume of the tree which, from the viewpoint of flotation, is unfortunate, as it is fairly and more or less uniformly dry. In larger trees, fungus infection is very common indeed, and infected wood is much wetter.

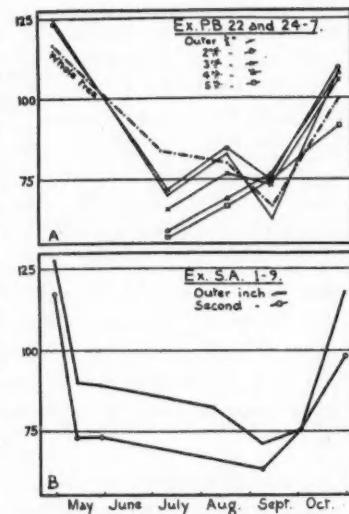


FIG. 10. *Poplar. Decrease in water content during the summer of 1931, as shown by borings.*

A. *On the Price Brothers limits, trees 8 in. D.B.H.; borings to a depth of two and a half inches. Water content of whole tree by disc method added for comparison.*

B. *Near Ste. Anne de Bellevue. Borings to a depth of two inches. Trees 8 to 15 in. D.B.H.*

any marked seasonal variation (but see individual growth ring analyses). This is contrary to the findings of Hartig (15-17) for *Pinus sylvestris* in Europe. Table V gives a very brief summary of the results.

TABLE V
WATER CONTENT OF JACK PINE

Date	Position in tree	Water content					Remarks	
		Sapwood			Heartwood			
		Outer	Mid.	Inner	Outer	Centre		
1929	Average of all pieces	139	—	144	32	37	Analyzed after some delay.	
	Average of all pieces	148	—	132	30	32	Analyzed after some delay	
	Average of all pieces	141	124	103	33	32	Analyzed after some delay	
	Average of all pieces	160	—	147	33	34	Analyzed after some delay	
1930	Average of all pieces	161	—	148	32	33	Analyzed in bush	
	Average of all pieces	138	135	131	35	34	Analyzed in bush	
1931	Tops	179	170	179	38	36	Three trees.	
	Middles	173	177	174	34	35	Analyzed in bush	
	Butts	164	164	164	35	35		
	Average	172	170	172	36	35		

There is very little difference in water content between the sapwoods of top, middle and butt logs. Top logs, of course, are wetter as a whole because of the higher proportion of sapwood.

The maximum possible water content of jack pine is about 205% (based on dry weight) and values approximating this have been obtained in outer sapwood.

5. SPRUCE (*Picea canadensis*)

The results are summarized in Table VI. As in jack pine, there is no appreciable change in water content throughout the year. The upper parts of the tree seem to be a little wetter than the lower parts (quite apart from the question of proportions of heartwood and sapwood). The amount of water in the heartwood is remarkably constant, but probably just sufficient to saturate the cell walls, as in jack pine. For the distribution of water in the outer growth rings see Fig. 6 and below.

TABLE VI
WATER CONTENT OF SPRUCE

Date	Position in tree	Water content					Remarks	
		Sapwood			Heartwood			
		Outer	Mid.	Inner	Outer	Centre		
1930	Average of all pieces	160	—	115	42	44	Slight delay in analysis	
	Average of all pieces	—	171	—	—	40		
	Average of all pieces	181	177	137	42	48		
1931	Jan.	Tops	166	170	139	42	46	Three trees. Analyzed in bush
		Middles	159	160	138	43	40	
		Butts	146	146	127	41	40	
		Average	157	159	135	42	42	
	July	Tops	182	146	132	43	41	Three trees. Analyzed in bush
		Middles	174	154	131	39	45	
		Butts	161	122	112	35	38	
		Average	172	141	125	39	41	
	Aug.	Tops	192	166	144	—	39	Three trees. Analyzed in bush
		Middles	179	156	120	39	42	
		Butts	165	146	124	37	48	
		Average	179	156	129	38	43	
	Sept.	Tops	198	178	144	44	44	Three trees. Analyzed in bush
		Middles	181	162	141	41	40	
		Butts	187	170	148	35	40	
		Average	189	170	144	40	41	

6. BALSAM (*Abies balsamea*)

The results are summarized in Table VII. Balsam, of the trees investigated, has the highest water content, averaging well over 200% in the sapwood as a whole. The average maximum possible water content of this tree is about 260%. Actually, figures in excess of 300% have been recorded and the figure of 260% is commonly met with. The gas content of the sapwood of balsam, therefore, is very low indeed.

The heartwood of this tree presents a curious problem. It is never (?) uniformly dry, but has irregular wet patches which are commonly associated with "blind knots" and small branches but do not follow these exclusively. The line of demarcation between wet and dry wood seems almost invariably to be very sharp and connection between these wet zones and the sapwood has not been observed. On the contrary, a complete, relatively dry ring usually is evident between the two. The water content of the driest heartwood probably represents water of wall saturation, while the water content of the wet patches is about that of the sapwood, and it would be natural to

TABLE VII
WATER CONTENT OF BALSAM

Date	Position in tree	Water content					Remarks	
		Sapwood			Heartwood			
		Outer	Mid.	Inner	Driest	Wettest		
1930	Average of all pieces	—	197*	—			Slight delay in sampling	
	Average of all pieces	—	213*	—				
	Average of all pieces	222	213	191				
1931	Tops	186	179	182	77	209	Three trees. Sampled in bush	
	Middles	215	213	196	47	220		
	Butts	189	199	185	43	253		
	Average	197	197	188	—	—		
	Tops	264	208	184	63	88		
July	Middles	269	210	174	60	168	Two trees. Sampled in bush	
	Butts	252	206	184	38	239		
	Average	262	208	181	—	—		
	Tops	257	224	186	—	—		
Aug.	Middles	271	237	209	32	—	Two trees. Sampled in bush	
	Butts	268	241	196	41	—		
	Average	265	234	197	—	—		
	Tops	223	215	189	116	180		
Sept.	Middles	251	229	208	42	246	Three trees. Sampled in bush	
	Butts	248	211	190	42	287		
	Average	241	218	196	—	—		

*Average for all parts of sapwood.

suppose that these regions represent continuing patches of sapwood, but the evidence from girdled trees is against this (see below). The sapwood of balsam is, as in most trees, much more permeable to water than the heartwood. The wet patches of the heartwood, while somewhat more permeable than the dry, fall far short of the sapwood in permeability. In two trees examined, absolutely no correlation between the position of these wet areas and orientation of main branches and roots could be found. In cases of fungus infection, the wetness precedes the fungus infection. It is not, as in red heart of birch, a result of it.

7. LARCH (*Larix laricina*)

The distribution of water seems to resemble that in spruce. In January 1930 three trees had an average water content in the sapwood of about 150% and in the heartwood of about 60%, while the distribution of water in the outer growth rings was almost exactly the same as in spruce (Fig. 6).

In view of the deciduous character of larch it would be interesting to follow its water content throughout the year, since it may be expected (unlike spruce, balsam and pine) to show decided seasonal changes. Th. Hartig, indeed, has recorded a summer drop in water content of *Larix europaea* in Europe and its transpiration is relatively high.

Diurnal Variations in Water Content in the Living Tree

Considerable variations of water content within twenty-four hours have been reported by several workers. Th. Hartig obtained higher figures at night and Kraus (18) recorded similar fluctuations: "Pflanzenteile sind am Tag kleiner, bei Nacht grösser . . . Diese An- und Abschwellung resultiert aus dem periodisch schwankenden Wassergehalt der Theile; dieser ist regelmässig am Tage geringer, in der Nacht höher."

In the course of the present studies a number of observations have been made. Results obtained in 1931 are summarized in Tables VIII-XI.

TABLE VIII
BIRCH (EXPERIMENT No. P.B. 24)

Date	July 9		July 10
Time	7:30 a.m.	11:30-12 noon	6:30-7 a.m.
Weather conditions, etc.	Fine, after fine weather.	Fine.	Dull and damp, after heavy rain.
Outer half inch	69	63 (-10)	85 (+38)
Inner half inch	68	59 (-12)	80 (+40)

Borings at breast height to a depth of 1 in. in two $\frac{1}{2}$ in. sections. In this and Tables IX-XIII unbracketed figures are water contents based on dry weight, while bracketed figures represent percentage changes from the previous figures. Figures are averages from four trees.

TABLE IX
BIRCH (4-5 IN. D.B.H.) (EXPERIMENT No. S.A. 6)

Date	August 8			August 9	
	9 a.m.	12 noon	6 p.m.	9 a.m.	7 p.m.
Weather conditions, etc.	Hot, fine after fine spell.	Hot and fine.	Cloudy.	Very dull.	Very dull. Fresh breeze. Some rain.
Outer inch	58	60 (+3)	60 (0)	60 (0)	62 (+4)
Inner inch	62	59 (-5)	59 (0)	60 (+2)	60 (+1)

Borings taken breast-high to depth of 2 in. in 1 in. sections. Average of four trees.

TABLE X
BIRCH (6 IN. D.B.H., HEIGHT ABOUT 50 FT.) (EXPERIMENT NO. P.B. 25)

Date	Aug. 15	Aug. 16		Aug. 17	Aug. 19
Time	3 p.m.	5:15 a.m.	6:30 p.m.	6:30 p.m.	6 a.m.
Weather conditions, etc.	Fine.	Fine.	Fine.	Fair.	(Dull on Aug. 18.) Dull.
Top Butt	48 58	69 (+44) 80 (+38)	55 (-20) 66 (-17)	59 (+8) 70 (+6)	70 (+18) 70 (+1)

Bored at breast height ("butt") and about 30 ft. from the ground ("top") to a depth of one inch. Average of three trees.

TABLE XI
BIRCH (4-5 IN. D.B.H.) (EXPERIMENT NO. S.A. 7)

Date	Sept. 7			Sept. 8	
	9 a.m.	1 p.m.	6:15 p.m.	5 a.m.	9 a.m.
Weather conditions, etc.	Fine, sunny, cool, strong breeze.	As in the morning.	Fine.	Sunrise at 5:22 a.m. Fine.	Fine. Warmer than Sept. 7.
Outer inch	59	56 (-4)	61 (+8)	62 (+2)	59 (-5)
Inner inch	66	61 (-7)	66 (+9)	67 (+1)	62 (-7)

Bored at breast height to a depth of two inches. Average of four trees.

In the first experiment (P.B. 24, Table VIII) a substantial decrease occurred between 7:30 a.m. and noon. Heavy rain resulted in a marked upswing within the next 18 hr. In the second experiment relatively small and irregular changes were noted. In Experiment P.B. 25 (Table X) considerable fluctuations occurred. With some exceptions there were fairly close correlations between borings from breast height and from 30 ft. The last experiment of this series was carried out late in the season, when large changes would be unlikely.

The results from these series are not altogether conclusive. They are supplemented by two series carried out in 1932, the results of which are summarized in Tables XII and XIII.

Experiment S.A. 21 was carried out at a time when water contents were high, leaves not fully expanded and reserve water of the soil ample, and the changes appear to be minor ones.

The second series was carried out on August 24-25 during very hot weather. Very uniform figures were obtained just before sunrise on August 24. At 1 p.m. all four trees showed decreases of from 13 to 21% (average 17%), while at 7 p.m. increases (over the 1 p.m. results) of from 0 to 12% were

TABLE XII

DIURNAL CHANGES IN WATER CONTENT. BIRCH (4-5 IN. D.B.H. HEIGHT ABOUT 35 FT.).
(EXPERIMENT NO. S.A. 21)

Date	June 6		June 7			June 8
Time	2 p.m.	7:30 p.m.	4:30 a.m.	2 p.m.	7:30 p.m.	4:30 a.m.
Weather conditions, etc.	Fine, hot.	Fine.	Sunrise at 4:22 a.m. Cold, dull, windy.	Dull, slight shower	Fine.	Fine.
	76	84 (+11)	83 (-2)	84 (+3)	82 (-3)	84 (+3)

Bored breast-high to a depth of one inch. Averages from four trees.

TABLE XIII

BIRCH (4-5 IN. D.B.H. HEIGHT ABOUT 35 FT.) (EXPERIMENT NO. S.A. 22)

Date	August 24			August 25		
Time	5 a.m.	1 p.m.	7 p.m.	5 a.m.	1 p.m.	7 p.m.
Weather conditions, etc.	Sunrise 5:06 a.m. Fine.	Fine, very hot.	Fine.	Fine.	Slightly overcast.	Fine.
	65	54 (-17)	58 (+7)	59 (+3)	50 (-15)	53 (+6)

Four trees.

recorded. At 5 a.m. next morning substantially similar figures (but well below the previous 5 a.m. figures) were obtained. At 1 p.m. decreases of from 9 to 21% (average 15%) were found, and at 7 p.m. somewhat less uniform figures showed an average increase of 6%.

In spite of the limitations of the method it is clear that when marked diurnal fluctuations are recorded the results are similar, *viz.*, a maximum water content at, or perhaps some time before, sunrise, a rapid decrease during the morning and an increase during the afternoon and night. This, as will be seen in a later paper, agrees with other observations, notably those on leaf water contents and changes in diameter of trunks.

There is one point that calls for note here. If rapid fluctuations in water content may occur, how reliable are the seasonal figures recorded above? The answer is that most of the results are from trees cut during the middle and later parts of the day. Borings have been taken almost without exception in the early afternoon and thus are comparable. The agreement between results from borings and those from the whole tree removes all doubt as to the possible effects of diurnal fluctuations on these figures.

Water Content of Diseased Trees

In trees of 8 in. D.B.H., red heart may extend over a diameter of two to three inches at the butt and the infection may reach the top logs. Where red heart is extensive a second condition, a brown rot, is often present, and is sometimes found even when red heart is absent. Samples from the Price Brothers limits have been examined by Miss Fritz (10), who finds that red heart is almost certainly due to *Torula ligniperda*, while a variety of organisms, including *Fomes igniarius*, *F. fomentarius*, *F. pinicola* and *Pholiota adiposa* may be associated with rot.

Infected parts are almost always much wetter than normal, as noted by Gibbs (11). The volume affected is usually relatively small and the flotability of an infected log will be but slightly less than normal. Infection through wounds is quite rapid and leads apparently to a higher water content in most cases (see discussion in section on girdling).

Snell (33, 34) has shown that for certain woods there are limits of moisture content at which fungi will grow. His "inhibition point of decay" corresponds to an air content of about 20% (based on fresh volume) of the woods. The gas content of wood in the living tree may be much below this value. In birch and in the sapwood of poplar it rises above and falls below this figure, while in the sapwood of the conifers considered it is normally less than 20%. In the heartwoods of poplar and of the conifers it is always (in healthy wood and except in the wet patches of balsam) considerably higher. In red heart of birch there is often much less than 20% of gas present and this, according to Snell, might be expected to inhibit further growth of fungi, but it is doubtful if this is the case.

Artificial Control of Water Content by Girdling

The effects of girdling are due primarily to two factors: the isolation of the root system from the source of organic food supply and (when girdling is deep) interference with the supply of water to the upper parts of the tree. Two major reasons for the girdling of hardwoods on pulp limits have been advanced and a certain amount of experimental work has been carried out with a view to commercial application by Churchill (5), Westveld (35), and Plice and Hedden (25). Where softwoods are desired it has been suggested that regeneration of conifers after selective cutting may be aided by the slow removal of the remaining hardwoods, and girdling is an obvious and practicable way of effecting this. If at the same time the water content of the girdled trees be markedly reduced, then the dead timber may be floated successfully and utilized for pulping.

In February 1930, birches were girdled on the Price Brothers limits, all wood being cut away to a depth of about one inch. Results are summarized in Table XIV.

TABLE XIV
WATER CONTENT OF GIRDLED AND NORMAL BIRCH

Expt. no. Date, Remarks	Girdled			Normal			
	Tree nos. and parts	Distribution of water across tree		Expt. no. Date, Remarks	Tree nos. and parts	Distribution of water across tree	
		Outside to centre	Outside to centre			Outside to centre	Disc
P.B. 11, June 14, 1930 (i.e., girdled 4 mos.). Leaves nearly open.				P.B. 7, Feb. 20, 1930. Cut at time and place of girdling.	Average of 3 trees		
	1	86	83	78	91	99	88
	Top	83	84	86	88	115	89
	Mid.	91	93	97	113	143	94
	Bt. A	86	89	91	115	132	92
	Bt. B						
	2	94	95	96	100	99	98
	Top	93	91	94	103	127	97
	Mid.	94	87	94	108	119	94
	Bt. A	94	88	88	95	130	93
	Bt. B						
	3	57	78	84	91	101	78
	Top	86	88	90	101	108	88
	Mid.	86	88	98	127	134	94
	Bt. A	86	88	95	101	119	135
	Bt. B	89	95	101	119	135	94
	Averages	79	85	86	94	100	88
	Tops	87	88	90	97	—	91
	Mids.	90	89	96	—	—	93
	Bts. A	90	91	93	—	—	93
	Bts. B						

Bt. A = Butt sample above girdle; Bt. B = Butt sample below girdle. Figures in bold face are from blocks with red heart or with rot.

TABLE XIV—Continued
WATER CONTENT OF GIRDLED AND NORMAL BIRCH

Bi. A = Butt sample above circle; **Bi. B** = Butt sample below circle. Figures in bold face are from blocks with red heart or with rot.

TABLE XIV—Concluded
WATER CONTENT OF GIRDLED AND NORMAL BIRCH

Expt. no. Date, Remarks	Girdled		Normal		Disc	
	Tree nos. and parts	Distribution of water across tree Outside to centre	Expt. no. Date, Remarks	Tree nos. and parts		
P.B. 25, Aug. 15, 1931 (i.e., girdled eighteen months). Leaves yellowing.	1 Top Mid. Bt. A Bt. B	45 51 53 59 62 43 48 53 60 74 59 54 52 56 79 62 61 55 56 78	50 49 56 60	P.B. 25, Aug. 17, 1931. From same stand as P.B. 13.	1 Top Mid. Bt.	59 53 53 56 63 47 46 49 53 63 49 48 51 55 67
	2 Top Mid. Bt. A Bt. B	39 47 50 59 73 42 64 81 82 78 45 40 51 61 69 66 51 62 64 85	46 56 47 60	Top Mid. Bt.	63 58 59 62 70 54 53 55 57 65 51 49 53 60 100	
	3 Top Mid. Bt. A Bt. B	41 49 53 59 70 43 61 84 95 106 52 75 105 109 117 70 96 108 126 128	48 62 75 91	Top Mid. Bt.	56 53 55 57 65 56 55 55 63 75 64 56 63 59 101	
	Averages Tops Mids. Bts. A Bts. B	42 49 52 59 68 43 58 73 79 86 52 56 70 75 — 68 69 75 — 70	48 56 59 —	Averages Tops Mids. Bts.	59 55 56 59 66 52 51 53 58 — 55 51 52 58 —	

Bt. A = Butt sample above girdle; Bt. B = Butt sample below girdle. Figures in bold face are from blocks with red heart or with rot.

It will be seen that there is little difference in water content between normal and girdled trees. This is in agreement with the results of R. Hartig (15-17) for *Betula verrucosa* in Europe. The outer parts of trees above the girdle are definitely drier than those of the untreated trees, however, and this is certainly due to hindrance of the upward flow of water in these regions by the removal of the outer wood, but the reduction of water content is not sufficient materially to improve the flotability and even the slight improvement noted is counterbalanced by fungus infection.

While this may be a useful method of removing birch where softwoods are wanted, it is useless if utilization of the birch for pulpwood is desired. The results obtained are precisely as expected and one is forced to believe—experiments with dyes and on rapid fluctuations in water content seeming to confirm this—that the whole wood of the birch is available for water conduction.

Where there is definite heartwood and sapwood it has often been assumed that water conduction is confined to the sapwood. In poplar and balsam, however, where the heartwood, though drier on the average than the sapwood, contains a good deal of free water, it seems *a priori* possible that water can be carried through part at least of this region.

With a view to investigating the behavior of softwoods and particularly balsam, two trees of balsam and three of spruce were girdled on June 6, 1931, by cutting away all the sapwood in every case. These trees were felled and analyzed in September 1931. Results for balsam are summarized in Table XV.

TABLE XV
EFFECT OF GIRDLING ON WATER CONTENT OF BALSAM

Experiment no.	Treatment, etc.	Remarks	Nos. of trees.	Water content					
				Sapwood			Heartwood		
				Outer	Middle	Inner	Wet patches	Dry patches	
P.B. 23. Girdled June 6, 1931. Felled Sept. 15, 1931. All sapwood cut away.	Needles falling. Slight fun- gus infection (brown) near girdle.		1	Top	37	35	34	90	45
				Mid.	47	40	50	238	—
				Bt. A	36	37	33	262	72
				Bt. B	252	220	205	226	68
	Needles falling. Slight fun- gus infection (brown) near girdle.		2	Top	39	36	34	44*	36
				Mid.	45	55	47	160	47
				Bt. A	47	44	47	240	67
				Bt. B	276	241	212	266	55
Control P.B. 26. Freshly cut Sept. 15, 1931.	Water content substantially the same as that of girdled trees at time of girdling.		Average of three trees	-			-		
				Tops	223	215	189	180	—
				Mids.	251	229	208	246	42
				Bts.	248	211	190	287	42

Bt. A = above girdle; Bt. B = below girdle. *No wet patches.

The results from balsam are especially interesting. The sapwood above the girdles lost almost all free water but the heartwood still showed the characteristic wet regions noted earlier in this paper. These regions, then, cannot be considered as available for water supply.

The results from spruce were conflicting. In one tree almost complete drying of sapwood occurred but in the other two little change was noted. These were infected (subsequent to girdling) by a blue stain fungus. All three trees had substantially the same water content when girdled (borings were taken from different heights) and it is difficult to explain the results.

The experiment was repeated in 1932. Balsams behaved as in 1931 and three spruce trees showed various degrees of drying, but in no case did the sapwood remain as wet as in the two spruce trees examined in 1931.

The results for balsam resemble those obtained by R. Hartig (15-17) for oak (*Quercus pedunculata*) in Europe. He girdled two trees, removing a complete ring of sapwood in each case, and felled them one and five weeks after girdling. In each case the sapwood dried out very effectively while the heartwood was but slightly affected.

From the standpoint of floatability girdling is seen to be but partially effective. In the case of balsam, the top logs of which are notoriously poor floaters, girdling may be a remedy but it is questionable if it is a practical one. Birch is not materially improved. Spruce, with the exception of extreme top logs, floats well in any event and such drastic treatment as girdling would hardly be suggested for it.

Poplar, jack pine and larch have not been tested. The first has such a wide sapwood that removal would hardly be practicable, while jack pine floats fairly well and the quantity used, at least on the timber limits considered, hardly justifies investigation. The same may be said for larch.

Changes in the Water-Gas System of Trees and Logs during Seasoning and Flotation

In the previous pages the question of natural gas-water distribution in the living tree has been discussed. It remains to consider the changes which occur when the tree is cut and subjected to seasoning and flotation. It is obvious that the composition of the gas concerned as well as its volume will influence the rate of removal during flotation. MacDougal (19-21), and MacDougal, Overton and Smith (22) find that carbon dioxide is always present in amounts much greater than in the atmosphere (sometimes 60 times as great), while the amount of oxygen is much less, and the sum of oxygen and carbon dioxide less than in air.

It is not easy to determine variations in gas content since a decrease in volume of water may be followed by expansion of the gas present rather than by entrance of more gas. There are even workers who maintain that the conducting elements in the normal state contain water vapor rather than "gas" in the spaces not occupied by water. Scheit (29-32) believed this to be the case ("die wasserleitenden Organe entweder Wasser oder Wasserdampf, nicht aber Luft führen") and Priestley (personal communication) inclines to this view.

The very high tensions in wood vessels of the current year found by Priestley and confirmed by Scarth and Gibbs (unpublished work) show that the gas may be under extremely low pressure and it is quite possible that water vapor alone is sometimes present, a possibility that is rendered more likely by the quick refilling of vessels when transpiration is reduced.

Release of tensions, and of pressures when they exist, may lead to a change in the water-gas distribution in the tree, but the water contents of individual rings as determined from cut trees are so nearly equal, in top, middle and butt sections, as to suggest that the change, if any, is slight.

Fermentative and other changes, including those due to respiration of living cells in the sapwood, lead to changes in composition of gas in cut logs. This has been discussed by Boberg and Juhlin-Dannfelt (2, 3) and by Scarth and Gibbs (28). Scarth (27) testing wood from floated logs found very high concentrations of carbon dioxide.

(a) FIELD SEASONING OF BIRCH

Attempts have been made to follow (a) the reduction in total water content and (b) the change in both lateral and longitudinal distribution of water, since distribution of the moisture is obviously almost as important as the quantity present.

Experiment P.B. 13. Started in June 1930

1. Three birch trees were cut, and the amounts and distributions of water were determined. Four-foot bolts were sawn from these trees, alternate logs were barked, and both barked and normal logs were piled together in the bush.
2. Three trees were felled, the trunks peeled, and the whole trees left lying, with the leafy tops on, in the bush.
3. In October the water contents of the trees and logs were investigated and fresh trees cut for comparison (Table XVI).

TABLE XVI
FIELD SEASONING OF BIRCH, 1930 (EXPERIMENT P.B. 13)

Date, etc.	Remarks	Position in tree	Distribution of water						Total water
			Outside to centre						
June	Freshly cut. Three trees. Bolts used for C and D below.	Tops Middles Butts Average	98	92	92	93	102	98	
			95	90	93	99	111	94	
			88	87	89	104	142	93	
			97	90	91	(99)	(118)	95	
June-Oct.	Three trees cut same time as A. Peeled and left whole with tops on. Analyzed October.	Tops Middles Butts Average	31	33	35	34	33	34	
			33	37	38	38	40	35	
			35	40	44	50	93	40	
			33	37	39	41	(55)	36	
Oct.	Single tree felled in October. Analyzed at once.	Top Middle Butt Average	92	84	78	85	91	86	
			90	82	81	77	88	84	
			90	80	80	81	85	84	
			91	82	80	81	88	85	
Nov.	Three trees felled in November. Analyzed at once.	Tops Middles Butts Average	81	89	89	91	94	88	
			83	85	83	88	103	84	
			86	83	83	86	—	84	
			83	86	85	88	(98)	85	
June-Oct.	4-ft. bolts from A, with bark. Piled June-Oct. Analyzed in October.	Tops Middles Butts Average	Distance from end of log						Aver.
			75	81	81	89			
			59	74	80	89			
			68	79	84	91			
June-Oct.	4-ft. bolts from A, without bark. Piled June-Oct. Analyzed in October.	Tops Middles Butts Average	67	78	82	90			79
			59	36	37	37			
			56	42	42	42			
			56	44	45	45			
D			57	41	41	41			44

Figures in bold face include those from blocks with red heart; averages bracketed include such figures or are incomplete.

In the four months which had passed the standing trees lost very little water (95% in June, 85% in October). The "sour-felled" trees, i.e., those felled, peeled and left with tops on, however, had but 36% of moisture, the whole tree with the exception of the very centre of the butt being almost uniformly dry.

The peeled and unpeeled, piled logs, which had been piled on skids to keep them free of the ground, had lost very different amounts of water, the unpeeled logs having almost as much water as the standing trees (79 against 85), while the peeled logs had lost more than half their water (from 95 to 44%).

The first snowfalls of the autumn occurred while the October analyses were being made and very quick penetration of water (from early, wet snow) was taking place through cracks which had developed in the peeled logs and in the peeled sour-felled trees.

The summer of 1930 had been a relatively wet one, so the experiment was repeated in 1931 which proved to be a much drier year. The results are summarized in Table XVII.

TABLE XVII
FIELD SEASONING OF BIRCH, 1931 (EXPERIMENT P.B. 23)

Date, etc.	Remarks	Position in tree	Distribution of water					Total water
			Outside to centre					
June A	Three trees. Freshly cut.	Tops	80	80	80	83	93	79
		Middles	106	93	90	93	104	95
		Butts	105	94	90	99	128	100
		Average	97	89	87	92	(108)	91
June-Sept. B	Three trees cut at same time as A. Peeled and left whole with tops on. Analyzed in Sept.	Top*	52	42	43	43	46	42
		Middle*	29	32	37	36	36	36
		Butt*	33	37	41	63	89	37
		Average	38	37	40	47	57	38
July-Sept. E	Two trees felled in July. Both left whole with tops on. No. 1 peeled. No. 2 with bark on. Analyzed in Sept.	Top 1	—	—	—	—	—	48
		Top 2	—	—	—	—	—	59
		Mid. 1	36	35	38	37	38	37
		Mid. 2	47	44	47	50	56	45
		Butt 1	—	—	—	—	—	45
		Butt 2	—	—	—	—	—	43
		Average 1	—	—	—	—	—	50
		Average 2	—	—	—	—	—	50
Sept. F	Three trees felled in September.	Tops	54	55	57	57	67	56
		Middles	57	59	60	63	72	60
		Butts	69	70	72	77	82	71
		Average	60	61	63	65	74	62
June-Sept. C	4-ft. bolts from A (above) with bark, left piled in bush. Analyzed in September.	Distance from end of log					Aver.	
		Top†	61	73	79	77		
		Middle†	66	68	74	82	73	
		Butt†	68	77	81	84	76	
June-Sept. D	As C but without bark.	Average	65	73	78	81	74	
		Top†	47	37	37	39	40	
		Middle†	46	40	41	40	42	
		Butt†	47	46	47	48	47	
		Average	47	41	42	42	43	

*Top from tree 1, middle from tree 2 and butt log from tree 3 only, but total water calculated from all logs.

†Logs from trees 2 and 3 only.

During 1931 the standing trees lost very much more water than in 1930, otherwise results were much as in 1930. In both experiments the sour-felled peeled trees had shown the optimum seasoning and since in June it is remarkably easy to peel birch with a "spud" the method has certain advantages. It seems fairly certain that it is evaporation from the leaves that leads to the better seasoning of sour-felled trees.

Flotation tests which are described below were carried out in an effort to determine the fate of such seasoned logs.

(b) FLOTATION

1. *Top-drying*

Flotation under laboratory conditions may be a very different thing from flotation under commercial conditions. It must be remembered, however, that the passage of logs from the bush to the mill (the "drive") is not always a continuous process. Logs in the Shipshaw river, for example, may be boomed for months in Lac Onatchiway before being cut into shorter lengths ("slashing") for driving to the mill at Kenogami. Here there might well be a great measure of top drying similar to that observed in early laboratory experiments (Scarth and Gibbs (28)). Analysis of logs from the boomed timber did not confirm this but indicated rather that there must be considerable turning of logs during flotation. This was estimated on a small scale by booming a set of marked logs during the summer of 1931. These were selected in part from timber which had already been in the early part of the drive and in part from freshly cut material. The logs were first boomed in June and examined in July, August and September. Of the thirty logs floated, no fewer than nine (or 30%) had turned to some extent before September and analysis of several of the logs, including turned and unturned samples, indicated very little top drying.

2. *Experiments under Laboratory Conditions*

Experiments designed to test the relative importance of end and side penetration were described in an earlier paper (28). End penetration is of great importance and it was shown that painting would very considerably reduce penetration, although, when solution and exodiffusion of enclosed air are the limiting factors, end penetration is of less significance (27).

The rapid seasoning of peeled logs very naturally led to an investigation of their behavior during flotation, while the question of end penetration suggested a consideration of log length.

(a) *Barking and painting (birch and balsam).* Each freshly cut log, as received, was examined for water content and divided to form a pair, as follows:—

Birch Log 2A—Floated with bark.

2B—Floated after peeling.

5A—Peeled, ends painted, then floated.

5B—Peeled, sides painted, then floated.

8A—Peeled (discarded by accident).

8B—Peeled, painted all over, then floated.

The series was started in November 1930 and increase in weight was recorded at irregular intervals until early October 1931. At this time only one log (8B) remained afloat; 5B started to sink in January, while the other logs were all down by the end of April.

Balsam Log 2A—Barked, ends painted, then floated.
 2B—Barked, sides painted, then floated.
 5A—Floated with bark on.
 5B—Barked, painted all over, then floated.
 8A—Barked, then floated.
 8B—Barked, then floated.

The results from both series are summarized in Fig. 11, in which increase in weight, expressed as a percentage of the weight when floated, is plotted against time. In each series the lowest curves (8B and 5A in 11A; 5B and 2A in 11B) are those for logs with painted ends. These show approximately a straight line relation between increased weight and time of flotation. The curves for all other logs indicate a more rapid intake of water in the earlier stages of the experiment, followed by a decreasing rate of penetration. In 5A (series B), indeed, there was actually a slight decrease in weight during the summer. This was probably due to evolution of gas by fermentation (see 2 and 3).

Evidently removal of bark from unseasoned logs has very little effect on the rate of penetration of water (2A and 2B of the birch series). Later experiments with seasoned logs yielded somewhat different results (see below). The prevention of top drying which follows painting of the sides of logs is evident in the case of Log 2B in the balsam series. It is less obvious in Log 5B of the birch series, but even there it is clear that the water content is still rising steadily in October, while the rate of increase of weight of the other logs is falling off.

(b) *Barking, painting and log-length (birch and balsam).* One-, two- and three-foot sections were cut from eight-foot logs. The treatments and results are given in tabular form in Tables XVIII and XIX.

The conclusions to be drawn from the figures are not altogether clear. This is due in part to the limitations imposed by the nature of the experiments. Certain facts, however, are clear. The longer logs season more slowly than the shorter ones but the difference after 100 days under these conditions, in a fairly cool, well ventilated room, is slight. Logs from which bark has been removed show no difference due to log length at the end of this time. Barked logs season more rapidly than normal logs. When floated,

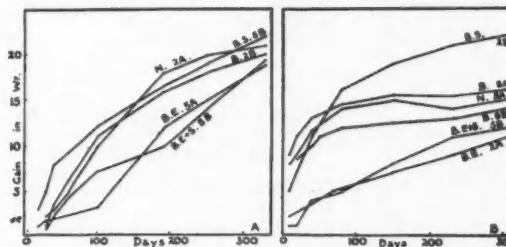


FIG. 11. Increase in weight of floated logs. Birch series A, balsam B. Letters on curves: B=barked. N=normal (with bark). E=ends painted. S=sides painted. E+S=ends + sides painted.

there is a certain amount of side penetration which is reduced by painting. In the present series there was prolonged seasoning and almost no top drying during flotation, so that the effects of side painting in preventing side penetration are clearly brought out. In the previous series, with unseasoned logs, top drying was extensive. The very marked effect of end painting is evident here, more especially in the balsam series.

TABLE XVIII
SEASONING AND FLOTATION OF BIRCH, 1931. EFFECT OF LOG LENGTH. EXPERIMENT
STARTED MARCH 8

Log nos.	Days from beginning of experiment to date	Treatment, etc.	Weight as percentage of original weight	
			1-ft. log	3-ft. log
A1* and A2	60 (May 7) 110 (June 26) 134 (July 20) 210 (Oct. 9)	Seasoning with bark on Seasoning with bark on Seasoning with bark on. Then floated July 20 **Flotation about $\frac{1}{2}$ in.	76 72 70 106	84 80 78 100
B1 and B2	60 (May 7) 110 (June 26) 134 (July 20) 210 (Oct. 9)	Seasoning without bark Seasoning without bark Seasoning without bark. Then floated July 20 Both sunk before Oct. 9	65 64 64 113	68 66 65 116
C1 and C2	60 (May 7) 110 (June 26) 134 (July 20) 210 (Oct. 9)	Floated from March 7 with bark on. C1 sunk, C2 with one end down. Both logs had sunk Both logs had sunk Both logs had sunk	114 119 120 121	107 115 117 121
D1 and D2	60 (May 7) 110 (June 26) 134 (July 20) 210 (Oct. 9)	Seasoning without bark Seasoning without bark Seasoning without bark. Then sides painted and floated on July 20 D1 had $\frac{1}{2}$ in. flotation, D2 had one end down	67 66 66 117	68 66 66 117
E1 and E2	60 (May 7) 110 (June 26) 134 (July 20) 210 (Oct. 9)	Seasoning with bark on Seasoning with bark on Seasoning with bark on. Then ends painted and floated on July 20. E1 flotation 1 in., E2 flotation $1\frac{1}{4}$ in.	74 70 69 84	81 76 75 93

* The first log of each pair is the 1-ft. log, the second the 3-ft. log.

** "Flotation" indicates amount of log above water.

TABLE XIX

SEASONING AND FLOTATION OF BALSAM, 1931. EFFECT OF LOG LENGTH

Log nos.	Days from beginning of experiment to date	Treatment, etc.	Weight as percentage of original weight		
			1-ft.	2-ft.	3-ft.
A1*, A2 and A3	50 (May 7) 104 (June 29) 206 (Oct. 9)	<i>Seasoned with bark on</i> <i>Seasoned with bark on. Floated July 4.</i> Flotation: A1 = 1 in., A2 = 1½ in., A3 = 1¾ in.	59 50 91	63 53 81	71 58 78
B1, B2 and B3	50 (May 7) 104 (June 29) 206 (Oct. 9)	<i>Seasoned without bark</i> <i>Seasoned without bark. Floated July 4.</i> Flotation: B1 = 1 in., B2 = 1½ in., B3 = 1¾ in.	48 46 97	49 46 88	50 47 93
C1, C2 and C3	50 (May 7) 104 (June 29) 206 (Oct. 9)	<i>Floated March 17 with bark</i> Floating C1, one end down Flotation: C2 = ½ in., C3 = ½ in.	123 124 126	118 120 122	117 120 122
D1, D2 and D3	50 (May 7) 104 (June 29) 206 (Oct. 9)	<i>Seasoned with bark</i> <i>Seasoned with bark. Barked and floated on July 4.</i> Flotation: D1 = ¾ in., D2 = 1½ in., D3 = 1¾ in.	62 50 88	70 58 72	75 64 71
E1, E2 and E3	50 (May 7) 104 (June 29) 206 (Oct. 9)	<i>Seasoned without bark</i> <i>Seasoned without bark. Sides painted then floated on July 4.</i> Flotation: E1 = 1½ in., E2 = 2½ in., E3 = 1¾ in.	48 46 89	54 48 74	55 48 75
F1, F2 and F3	50 (May 7) 104 (June 29) 206 (Oct. 9)	<i>Seasoned with bark</i> <i>Seasoned with bark. Ends painted then floated on July 4.</i> Flotation: F1 = 3 in., F2 = 2½ in., F3 = 2¾ in.	63 53 60	74 61 66	75 60 63
G1, G2 and G3	50 (May 7) 104 (June 29) 206 (Oct. 9)	<i>Seasoned with bark</i> <i>Seasoned with bark. Barked, sides painted then floated on July 4.</i> Flotation: G1 = 1½ in., G2 = 1½ in., G3 = 2½ in.	53 46 78	57 49 69	65 56 69

* In each group the first log is the 1 ft., the second the 2 ft. and the third the 3 ft. log.

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STUDIES OF WOOD

III. ON THE PHYSIOLOGY OF THE TREE, WITH SPECIAL REFERENCE TO THE ASCENT OF SAP AND THE MOVEMENT OF WATER BEFORE AND AFTER DEATH¹

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Abstract

The various theories of the ascent of sap are discussed and it is concluded that the tension hypothesis best meets the observed facts. Seasonal and diurnal variations in water and gas content and the changes in tension that are demonstrable are all in accordance with the demands of the tension hypothesis. The two greatest problems are probably the maintenance in conducting channels of continuous water columns under high tensions without entry of air, and the refilling with water of such channels as do become gas-filled during the summer (for the insulation of gas and water channels one from the other is apparently not perfectly maintained). These problems are not entirely settled, though the hypotheses of Münch and/or Lund may account for the refilling of vessels in deciduous trees during the non-leafy season.

The observed differences in the behavior of maple, birch and poplar during the period of sap flow have received attention. These peculiarities cannot be accounted for by differences in the root systems. The earlier cessation of bleeding and the development of tensions in poplar are correlated with a higher rate of evaporation from the twigs of the former, and this evaporation probably is largely through lenticels.

The problem of sinkage, in the light of this work, is briefly reviewed.

In a previous paper (55), the results of work on water content of trees and on the changes in water content that follow cutting have been presented. It remains to discuss these results in the light of present day knowledge of the physiology of the tree, and the discussion may well open with a consideration of theories bearing on the ascent of sap.

a. The Living Cell ("Vital") Theory

It is customary to consider that the works of Malpighi (see Sachs (141) and Grew (58, 59)) in the 17th century mark the beginnings of the science of plant physiology. It was natural in such "vitalistic" times that Grew should postulate a pumping action by living cells—an action that is still considered by a minority of workers in this field to explain the ascent of sap. Grew undoubtedly considered that sap flow, in part at least, took place in the "bark" (phloem and cortex) but he recognized that the wood also contains water at certain times: "For in the beginning of spring, it (the sap) riseth, neither betwixt the Wood and Bark, nor in the Bark; but only in the Wood."

His theory as to the ascent of sap, however, would seem to apply to the bark, and his "vessel" is not to be confused with a "wood vessel" as understood today. It is significant that he dismissed capillarity as an adequate force and regarded the parenchyma cells surrounding the "vessels" as pumping water into them.

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Westermaier (197, 198) decided that the conducting system of woody plants consists either of living wood parenchyma or of a combination of living and dead cells. Godlewski (57) differed on some points from Westermaier: "Nach mir . . . Hadromzellen im Holze nur als Stempel der Saugdruckpumpen . . . die Gefäße . . . die Röhren . . . nach Westermaier die Hadromzellen die Strombahn des Wassers selbst, und die Gefäßen . . . als Reservoir." Godlewski's theory was adversely criticized by Zimmermann (207). Westermaier evidently regarded the wood parenchyma ("hadrome") cells as the conducting tissue, while Godlewski thought of the wood vessels as carrying out this function and the parenchyma cells as supplying them with water—an entirely different thing when considered from the standpoint of the velocity of conduction. The rate at which water actually moves is, of course, very important when considering the manner of conduction. Huber (77) slightly warms a small region of the stem and then detects the propagation of the wave of increased temperature by means of tiny thermocouples. This probably gives one of the closest measurements of the actual rate and with it he has obtained a value as high as 75 cm. per minute—a velocity that is many times the possible maximum of diffusion from cell to cell.

A number of investigators, including Bierberg (9), who estimated that protoplasmic streaming accelerated movement of water three to four times, and Hugo de Vries (195), have postulated protoplasmic streaming as a factor in hastening transfer of water and solutes, but even with the most rapid streaming observed the rate of transfer could not be adequate.

Many others have concluded that living cells play some part in sap ascent. The views of Janse (83, 84), for example, are very much like those of Westermaier and Godlewski referred to above. In his early work, Ursprung (181), later a staunch supporter of the tension hypothesis, decided after a study of about twenty woody plants, that with the possible exception of *Sorbus aucuparia*, living cells played a part in all cases. C. H. Schultz (151) believed vital processes entered into the phenomenon, as did Boehm (14), Nordhausen (121) and Reinders (133, 134). Eames and MacDaniels (41, p. 68) say that "Histological evidence strongly suggests that the presence of living cells is necessary to the upward conduction of water by tracheids and vessels. Every water-conducting cell is in contact in some part of its wall surface with one or more living cells, and abundant pits are present in this contact area."

Ranged against these are many opponents of vitalism. Vesque (194) and Strasburger (168, 169), in his classic experiment with poisoned trees, presented arguments against the "vital" theory, while E. F. Smith (157) and Overton (122) observed flow of water through dead stems. Curtis (25, 26, 27) chilled petioles to check translocation and noted that movement of water was not appreciably decreased, an observation which it would be hard to reconcile with transfer by living cells. Zijlstra (205), nineteen years earlier, noted a similar lack of effect in *Helianthus* (Curtis used *Phaseolus vulgaris*), while Polunin (125) found that roots of *Betula odorata* conduct water at 0° C. Smith, Dustman and Shull (158) also refuse to believe that living cells have a role in sap ascent.

Although water will continue to pass through a dead stem for some time, the flow frequently decreases and becomes inadequate. The vitalists claim that this is due to the absence of living cells, the non-vitalists declare that the cause is occlusion of the dead water-conducting cells by material derived from the cells killed by the experiment. Not only are the living cells of no use in sap ascent, but in their death they prevent it! Dixon (31, 32) and his co-worker, Joly (36, 37, 38, 39), have given much thought to the question. Dixon concludes that the changes occurring above the killed section are due to the toxic action of the sap from the dead cells rather than to the cutting off of the water supply.

b. The Imbibition Theory

The fact that the cell walls of wood readily absorb a considerable amount of water led early investigators to believe that movement of water takes place in the walls. Unger (179, 180), and Wiesner (200) were among the supporters of this "imbibition theory" and Sachs (141) in his early work also believed in it, but he recanted later. Elfving (44), who investigated the relative movement of water in the radial, tangential and longitudinal directions, argued against imbibition as did Boehm (14).

Work on the changing water-content of floating logs, during which top-drying to well below the fibre saturation point has been noted, and the persistence of free water in the wet patches of balsam heartwood (Gibbs (55)), prove that the movement of water under such conditions is far from easy. Although imbibition may have relatively little to do with the ascent of sap it is by no means unimportant in the general economy of the plant, as Shull (155) and Woodhouse (202) point out.

c. The Capillarity Theory

Although the height to which water will ascend by capillarity in tubes of the diameter of wood vessels is insignificant when compared with the heights to which it rises in trees, many of the early investigators were misled by conditions in the tree and considered that capillarity could explain the ascent of sap. The presence of numerous air bubbles alternating with short columns of water (the so-called "Jamin chain") was supposed to decrease the effective hydrostatic head and make possible the easy ascent of water to heights exceeding that of a continuous column of water balanced by atmospheric pressure. Jamin (82) is usually credited with (or blamed for) the development of the theory. He stated, in a paper dated 1860, that "les forces capillaires suffisent pour expliquer le mouvement de la sève". Schwendener (153, 154) considered the process from the practical and from the mathematical viewpoints and supported Jamin. He took borings from pine, beech, etc. and found air and water in the vessels. Zimmermann (206), who seems to have criticized all the theories then current, failed to agree with Jamin. In the same year Vesque (193) published the results of observations on *Tradescantia zebrina*, and claimed that air obstructs rather than aids the movement of water in the vessels, while Pappenheim (123) noted that air bubbles in tubes may not move and attempted without success to demonstrate the

movement of water past the bubbles, though Strasburger (168) claimed (as did Copeland (23) later) that water does pass bubbles in the tracheae. The last remarks that if the bubbles moved the whole problem would have been solved by Malpighi! All recent work would seem to condemn the Jamin chain hypothesis.

d. The Distillation Theory

It has long been known that "tensions" may exist in the vessels of rapidly transpiring trees. If water be supplied from below and removed from above—with air or water vapor under low pressure between—then a relatively rapid distillation may occur. Scheit (145, 146, 147, 148) seems first to have advanced this "distillation theory". Priestley (personal communication) considers that it may play a part, and it is true that some vessels of rapidly transpiring trees may contain air under very low pressure—or perhaps nothing but water vapor. Against the theory, however, is the fact that substances in solution rapidly ascend to the tops of trees more than 32 feet high.

e. The Liquid-tension Theory

The idea that liquids might be drawn up to considerable heights by suction from above met with much opposition on the ground that the maximum height would be (for water) but little over 30 feet. In 1850, however, Berthelot (8), experimenting with a closed tube full of liquid, found that the liquid on cooling did not part from the tube and leave a "Torricellian vacuum" but "dilated" and continued to fill the tube. It was soon shown that the "tensile strength" of water actually amounted to several hundred atmospheres but the facts were not at once applied to biological theory, though Spencer (160), in a curious paper which postulated wind-produced oscillation of the tree as effective in causing sap ascent, said that: "A state of capillary tension must result . . . resisted below by liquid cohesion". In 1893, Boehm (15) claimed to have observed the lifting of mercury to over 90 cm. by a transpiring *Thuja* twig. His experiments were followed by those of Dixon and Joly (36, 37, 38, 39) who boldly proclaimed that *ascent of sap is brought about by evaporation from the leaves acting through liquid columns under tension and that the presence of dissolved air does not destroy the continuity of the columns*, and Askenasy (1, 2) who demonstrated a lift of more than 82 cm. of mercury by evaporation from a plaster-filled tube and applied the idea to ascent of sap.

The tension theory presents a number of grave difficulties. First of all is the need for the demonstration of *continuous water columns from leaf to root*. These, if present, may be very easily ruptured and this is one of the major arguments against the cohesion theory. Ursprung (183), in 1913, claimed that sap had very little tensile strength, but Dixon (33) found it able to withstand tensions of more than 200 atmospheres, nor did dissolved air decrease this very significantly. Measurement of the tensile strength of the liquid in the fern annulus and in the elators of a liverwort (*Lophozia*) were made by Renner (135), whose figures agree very closely with those of Dixon, while Ursprung (187) in his later work found tensions up to 300 atmospheres in fern annuli.

Water can be drawn up by evaporation from a porous clay surface, or even from a living twig, using a long, unobstructed tube or one filled with plaster of Paris, and lifts of more than 76 cm. (using mercury) may be obtained. The experiments of Askenasy have been mentioned above, but see also Livingston (96), Ursprung (182, 183, 184, 186) and Nordhausen (119, 120, 121). Copeland (23) described an artificial tree, complete with branches, of plaster-filled tubes, and his comments on the operation of this deserve quotation: "The positive result of our experiment is that the water column being continuous, but air being present, a suction of less than one atmosphere can still operate as a suction more than 12 metres down." (p. 166). And "This artificial tree had so much in its behaviour in common with real trees that when all was done I was likewise unable to explain it." Dixon, however, showed that the rate of transfer in Copeland's tree was hopelessly inadequate.

But to return to the subject of continuous water-columns. Bode (13) found unbroken columns in *Impatiens*, *Zebrina pendula*, *Cucurbita*, *Elatostemma*, etc. By direct microscopic examination he observed the movement of sap in the vessels and saw no air bubbles at all in uninjured water-conducting cells. He realized that some vessels may contain gas, but considered the actively conducting cells to be completely filled with water. Holle (72) some years earlier had found continuous water columns in other plants. The work of MacDougal (102, 103), MacDougal and Shreve (105) and MacDougal, Overton and Smith (104) also points to the existence of continuous water columns (see below).

Observations on the water content of birch at different seasons, and on the amount of water in individual year-rings of birch, larch, balsam and spruce indicate that the columns of water are continuous in these cases also. The similar water content of birch, at breast height and at 20 feet from the ground (Table I), certainly points to this conclusion.

TABLE I

BIRCH AT STE. ANNE'S (D.B.H. 4-5", HEIGHT ABOUT 30 FEET). BORED AT BREAST-HEIGHT (BUTT) AND AT ABOUT 20 FEET FROM THE GROUND (TOP) TO A DEPTH OF ONE INCH

Date, time	Position in tree	Water content of individual borings										Averages	
		Tree no.											
		1	2	3	4	5	7	8	A	B			
May 3 1-2 p.m.	Top Butt	88 83	102 104	101 98								97 95	
May 14 2-3 p.m.	Top Butt				87 88	82 80	79 76	99 94				86 84	
May 19 2-3 p.m.	Top Butt				78 82	72 78	80 68	81 80				78 77	
Aug. 25 1-2 p.m.	Top Butt	54 53	45 51	51 52								50 52	
Oct. 1 2-3 p.m.	Top Butt								58 48	53 58		56 53	

It is realized, of course, that practically uniform water content might result from a purely random distribution of very short columns, but it would appear unlikely that this would be maintained so constantly. The surprisingly uniform results obtained from the same rings at different heights in the tree (Fig. 1) are also of interest in this connection.

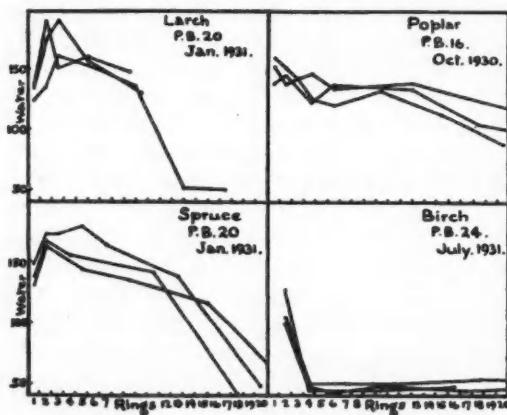


FIG. 1. Water in annual rings of several trees. Each set of three curves represents results from top, middle and butt samples. The numbering of rings is from the outside.

demonstration of very high tensions. Unfortunately this issue has been much confused, since few of the actual workers seem to have realized that the complex organization of the stem is such that separate (and largely independent) systems may exist side by side at one and the same time. Manometer measurements, which have been largely quoted, are evidently of little value. Since the time of Boehm (14, 15) many have attempted to demonstrate tensions and some of this work has already received notice above. Ursprung (188) claims to have demonstrated the formation by tension of continuous mercury columns of more than 76 cm. in branches of *Clematis vitalba*, using X-ray photography to record his results, while Thut (173, 174) obtained lifts, using living twigs attached to glass tubes after the manner of Boehm, of as much as 226.6 cm. of mercury (ca. 3 atm.). Nordhausen (120) attempted to measure the suction by comparing the rate of flow induced by the living twig with that produced by a pump of known efficiency and attached to the same stem as the twig, obtaining values up to 8 atm. by this means, while Renner (136) obtained a maximum value of 9 atm. for *Forsythia*.

When tensions are developed in the cells, a corresponding flexure of the cell wall results, and this may be detected and measured (13). Measurements of diameter changes of trees have shown that increase in diameter during growth is not a steady thing but that rhythmic diurnal changes may occur. MacDougal and his associates, Overton, Shreve and Smith (104, 105), have used the "dendrograph" for such work and attribute the smaller, rhythmic fluctuations in the form of the curves obtained to tension changes. Kraus (90), as far back as 1881, noticed that stems shrink during the day and

Direct observation with the naked eye does not suggest the regularity of distribution of gas and water within the single ring observed by MacDougal (102, 103), but it is not difficult to reconcile this with the presence of continuous water columns (see also Baker and James (7)).

Another difficult problem associated with the tension hypothesis is the actual

swell again at night, while Friedrich (quoted by Büsgen (18)) correlated changes in stem diameter with evaporation and noted accompanying small diurnal changes in water content. Mallock (108) used a very ingenious optical method to detect such small variations in growth. According to Haasis (61), a progressive contraction may occur during the dry season in the case of Monterey pine (*P. radiata*) and redwood (*Sequoia sempervirens*) with small increases at night (but see also the discussion below on seasonal variations in conifers). The diurnal variations observed agree in general with the daily fluctuations in water content of the tree.

The development of high tensions introduces a new, and perhaps the greatest, difficulty associated with the tension hypothesis. This is the question of the *permeability of the wood to gas*. *How are the gas and water systems isolated? Why does not gas pass into the conducting vessels when the pull is developed?* Intimately connected with these questions is that of the conductivity of wood for water. Most of the measurements of conductivity have been made with relatively large pieces of stem or even with isolated chips of wood—but *the conductivity of the cut stem or the permeability to gas of a block of wood tells little of the state of affairs in the living plant*.

Groom (60) and Farmer (47) have compared the rates of flow in conifers and deciduous trees, while detailed investigations of different species have been made more recently by Holmes (73, 74) for hazel and ash, by M. and F. Rivett (139) for *Rhododendron ponticum* and *Ilex aquifolium*, by Inamdar and Shrivastava (78, 79) for some tropical species, by Furr (52) and by Malhotra (106, 107). It would appear from this work that the minimum pull required to draw water to the top of a tree is equivalent to a hydrostatic head of about twice the height of the tree, but if the conductivity of the actual conducting portion be less than that of the stem as a whole the figure will be still higher. This means that in a tall tree tensions of at least 20 atm. must be developed. Why does not gas pass into the conducting cells under these conditions?

Steinbrinck (167) claims to have forced air through walls (?) of wood with a pressure of about one atmosphere, as did Jost (87). Claussen (20) found that wood is increasingly permeable as its water content rises, and his results would seem to be confirmed by those of Porsch (127). In 1910, however, Tiemann (176) claimed that ". . . in the fresh green wood . . . the cells . . . (except the resin ducts and the vessels) are completely closed by the continuous primary wall . . . and that gases cannot be forced through this enclosing membrane, even at extreme pressures." He thought that the increased permeability of wood seasoned to below the fibre saturation point is due to the formation of minute slits in the walls, a view adversely criticized by Bailey (3, 4, 5, 6), who showed that the pit membranes (part of the "continuous primary wall" of Tiemann) are not entire but are perforated. They are greatly changed by drying but are not ruptured by a pressure of 250 lb. to the square inch. According to Bailey ". . . the valve-like action of the tori undoubtedly assists in retarding the entrance of air into the water-conducting passages". If the tori do not act, however, the surface tension

of the sap in the pit membranes can be overcome by pressures of less than 3 atm. Incidentally, Miss Wright investigated the pit-closing membrane of the lower gymnosperms (203) and found that in *Ginkgo*, which becomes a large tree, the torus may be only half the width of the pore, so that it could not exert a valve action.

The actual dimensions of the pores of the pit membranes have been established by Bailey (3, 4, 5, 6), Stamm (164, 165, 166) and others. They are of such a size that pressure of perhaps 3 atmospheres should cause passage of air (see below). During the course of penetration studies, Sutherland (172) came to the conclusion that ". . . little resistance to flow is encountered in pit membranes of sapwood, and that the tracheids themselves provide the greater part of the resistance." It is difficult to believe that this is so. Sutherland claims to have found no evidence of the tori acting as valves.

In a recent address (131) Priestley remarks: "In actual experiments we have failed to displace the liquid contents of closed hardwood vessels by air, using pressures of 15 atmospheres. . . . Pores of pits do not open on to inter-cellular spaces . . . the liquid contents of the tracheal elements may be under tension without the slightest likelihood of air being drawn in from the inter-cellular system of the wood . . ." Priestley is dealing with the living tree and not with isolated blocks of wood: his results are therefore much more likely to give a true picture of conditions in the tree and if his figure of 15 atm. be correct, tensions could lift water to at least 220 ft. (reckoning the necessary hydrostatic head at $2 \times$ height of tree) without drawing air into the conducting cells.

Let us return again to a consideration of the mechanism that produces the pull on the water columns of the stem. The general opinion would seem to be that the water columns of the vessels are continuous with the living cells of the leaf and that these cells suck water from the vessels. Ursprung and Blum have contributed a great deal to this subject and their conception of suction force ("saugkraft") as the effective force has made an understanding of the subject much easier. Some of Ursprung's work has been mentioned above and further details are to be found in other papers (185, 189) by him, by Ursprung and Blum (190, 191, 192) and by Huber (75, 76). Dixon (34) and Miss Ernest (45) criticize the methods for the measurements of "saugkraft" and consider that many of the values given in the literature are incorrect, owing to changes in tensions, etc. during the course of the measurements. Very high osmotic pressures, however, have been recorded in a number of cases. Among the most interesting of these are those due to Fitting (49) who studied many Sahara desert plants, no less than 21% of which had osmotic pressures of 100 atm. or more, and Harris, Gortner and Lawrence (64), working in the Arizona desert, who measured the depression of the freezing point of the sap of different classes of plants. The last obtained average values for Δ of 2.34 (equivalent to an osmotic pressure of 28 atm. for trees and shrubs, 1.733 for dwarf and half shrubs, 1.357 for perennial herbs and 1.227 for winter annuals.

Although there is abundant proof of very marked tensions in plants and of the importance of transpiration in developing these tensions, active secretion of water may occur in the absence of transpiration. The existence of an apparent transpiration stream in submerged aquatics suggests a secretion of water by the (morphologically) upper parts of the plant. Thut (175), however, concludes that ". . . the flow of water through the submerged plants studied thus seems to be due primarily to 'root-pressure'." Active secretion is not confined to aquatic plants, being well known in land plants as "guttation".

It is convenient to turn again to the question of water content of trees as the points that remain to be discussed can be considered in this connection.

Some of the earliest results are those due to Matteucci (110), who cut poplar during a rigorous winter and found an average of 60% of water in the root, 56% at four metres and 51% at eight metres. His figures are too few to be of much use. In 1876, Geleznow (53) published the results of numerous observations in Russia on *Betula alba*, *Populus tremula*, *Acer platanoides* and *Pinus sylvestris*, trees closely related to those studied and described in the second paper of this series (55). His results are somewhat irregular but he noted a summer drop in the case of the hardwoods, while the one conifer given (*Pinus sylvestris*) showed very small changes in water content. In their extensive studies on sap flow in the maple, Jones, Edson and Morse (86) give the following figures* for water content of maples: December, 31.5, March 15, 36.5 and April 28, 47%. This rise was followed by a rapid decrease after the buds opened. Büsgen (17) and his students noted diurnal fluctuations in water content. Their figures for larch are particularly interesting, as they suggest that larch behaves as do other deciduous trees rather than as a conifer.

What are the causes of the seasonal changes, and why do trees, growing apparently under the same conditions, differ one from another in their water relations?

Broadly speaking, the climatic factor is one of the most important of all. In temperate regions with a summer growth period and a winter rest, or in parts of the tropics where a dry season takes the place of the winter, there is a season of rapid transpiration and, usually, a water deficit, followed by a period during which either little change in water content may be expected or the deficit is made up. It is generally conceded that the deciduous habit is a response to this and that the evergreen habit involves xerophytism in some form. A re-examination of observations on water content from this point of view is of interest.

Birch and poplar agree in showing a high water content at leaf opening followed by a relatively rapid, but by no means uniform, decrease during the summer months. During 1931, for example, the water contents of birch and poplar dropped from 92% (early June) to 54% (August), and from 124%

*The figures were really due to Spaulding (159), to whom thanks are due for the loan of manuscript records.

(late April) to 68% (September) respectively. There is no doubt that this loss is due to evaporation from the leaves at a rate in excess of water absorption. In 1930, on the other hand, a much less marked fall occurred. What are the factors responsible for this difference? The answer is by no means certain, but among the major factors are precipitation and humidity.

The period June-July of 1931, during which the water content of birch fell from 92 to 54%, was not an unusually dry spell, nor was the humidity low. August 1931, however, was much drier than the same month of 1930, and this may explain in part the difference between the water content figures for the two years (54 and 81%).

A better explanation may be found in the very dry winter of 1930-31, a winter which left the water levels of rivers and lakes in many parts of Quebec at record low marks and which undoubtedly left the soil with poor reserves of water.

Following the fall in water content during the summer months, there is a rise during the autumn which is already in progress just before leaf-fall. The water content during the winter months, however, is not at a maximum, but remains (for birch) in the neighborhood of 80%, the rise to the peak of about 100% occurring in the spring. The reasons for this behavior might seem to be clear. Following leaf-fall (October), transpiration is reduced to a very low level while the roots are still able to supply water, but root activities are brought to a standstill soon after this when the ground becomes frozen. In the spring, as the ground thaws out before leaf opening, the roots are again active and the water content rises. The observed rapid fluctuations in water content during 24 hr., on the other hand, forces one to believe that a day or two of continued root activity could, if other conditions permitted, fill the tree after leaf-fall. However, when the rapid fluctuations are taking place, very great tensions are developed (*i.e.*, the actual amount of gas in the tree is low but may occupy a relatively large volume), while in the autumn months the gas rarely shows much less or much more than atmospheric pressure and is present in much larger amount. It is possible that additional water can enter only if this gas is removed by solution or otherwise.

The easy passage of air into and out of the pneumatic system has been noted by many workers, but it may have little to do with gas in the water conducting system, for in spite of Livingston's statement in his review (95) that ". . . all features of the rise of water in plants are generally cared for if we make the supposition that no vessel segment that has once lost its liquid is ever refilled", and Priestley's opinion as to water vapor in cells, it seems that a large proportion of the water-conducting elements do become gas filled during the summer. This is not an argument against the tension hypothesis, since it is easy to imagine that some of the water columns—presumably those in the widest vessels—rupture, and that gas enters, but would seem to be a matter of fact, for the tree may certainly contain a large volume of gas at or about atmospheric pressure, when no tensions are demon-

strable in the conducting system. Observations referred to above, on bleeding from birch in October 1931, when the water content was only about 80%, are in harmony with this.

How do the vessels refill? If sufficiently high root and/or bleeding pressures can be developed, then the physical side of the question is more or less answered though the origin of the pressures may still be puzzling. As a matter of fact there is no evidence that these pressures are adequate for really lofty trees.

Whatever be the causes of root pressure and bleeding, it would seem that they indicate positive pressures in part (or perhaps all) of the hydrostatic system. James and Baker (81), however, conclude, since exudation may proceed while water in vessels is under tension, that: ". . . the positive hydrostatic pressures associated with the exudation must therefore be limited to the cells with protoplasmic contents either in the wood or elsewhere."

In two papers on the mechanism of root pressure, Priestley (129, 130) stresses the importance of the endodermis and its control of entrance and exit of water and solutes from the stele, while Blackman (10) criticizes some of Priestley's views. Further work is reported by Priestley and North (132). While the anatomical evidence suggests that the endodermis plays a part in control of water and/or solute movement, there is some doubt as to its exact role, especially in view of the fact that in large trees there is no endodermis surrounding the greater part of the conducting system in the root.

There would seem to be an intimate relation between sap concentration and development of positive pressures, and this leads to a consideration of the physiological changes that are concerned with winter rest and spring activity, for sap concentration varies with these. Nearly fifty years ago, Schulz (152) noted the disappearance of starch from evergreens during the winter, and an apparent storage of tannin-like materials, while Suroz (171) considered that starch changes to oil, the starch reappearing when the vegetative season begins. It should be noted that a recent publication by Doyle and Clinch (40) throws doubt on the statement as to oil formation.

Fischer (48) made extensive studies of winter reserve stuffs and divided trees into classes. In hardwoods he recognized eight phases:—

1. Starch maximum in Autumn (from leaf-fall till October-November).
2. Decrease in starch (October-November).
3. Starch minimum (December-January-February).
4. Regeneration of starch in spring (March-early April).
5. A second starch maximum (April).
6. Rapid decrease in starch (April-early May).
7. A second starch minimum (Middle-end of May).
8. Summer starch manufacture (End of May until leaf-fall).

Lidforss (93) began to correlate such changes in evergreens with resistance to winter cold and was followed by Czapek (29), Schellenberg (149) and Leclerc du Sablon (140). The last-named agreed with Schellenberg rather than with

Fischer in believing that starch is transformed into hemicelluloses and not into sugar during the winter months. Fabricius (46) also criticized Fischer's views and Niklewski (118) concluded, since starch content is profoundly affected by temperature while fat changes are not, that ". . . der Prozess der Fettumwandlung kann also nicht direkt mit dem Prozesse der Stärkeumwandlung zusammenhängen." In 1907 Lidforss published a very important paper (94) on evergreens, in which he pointed out that all members of the evergreen flora (he studied 130 species belonging to 40 families) are sugar-rich but starch-free in winter, though most of them are starch plants in summer. The intensive study of cold and drought resistance which followed this paper has resulted in a voluminous literature which is somewhat outside the scope of the present discussion. Preston and Phillips (128) concluded that Fischer's classification into hardwood-starch and softwood-fat trees is hardly justified. Sinnott (156) attempted to analyze the factors governing the character and distribution of reserve foodstuffs and decided that the character of the reserve depends primarily on ease of water access to the storage region and that this may be correlated with the carriage of enzymes in the water. Tuttle (177, 178) attempted to induce experimental change of reserves in *Linnaea borealis* in Alberta, and found that temperature appeared to be of fundamental importance, but with Lewis (92) she found, while investigating *Picea canadensis*, that rhythmic changes are more or less independent of temperature. This seems to be supported by the observations of the same workers on *Pinus Murrayana*, *P. albicaulis*, *Abies lasiocarpa* and *Picea Engelmannii*. Riazantsev (138) found, however, that rearrangement of chloroplasts in spring in the leaves of evergreens depends on temperature rather than on time, while Pojarkova (126) remarked the close connection between starch changes and depth of winter rest.

Is the sudden manifestation of hydrostatic activity associated with root pressure, and is bleeding always and entirely a result of the changes discussed above? Such phenomena as autumnal bleeding of birch are evidence against this. At least two distinct types of bleeding occur, however, and they seem to be fundamentally different. Frey-Wyssling (51) stresses this in a recent paper and distinguishes as "bleeding" the withdrawal of water from uncut cells by the osmotic pressure of the cell sap of the cut cells, which are released from wall-tensions, and as "root pressure" the forcing of water into the vessels through the negative suction force of root parenchyma cells.* Wiegand (199) comes to somewhat similar conclusions and agrees with Jones, Edson and Morse (86) that gas expansion due to temperature changes cannot account for the flow of sap from *Acer*. He regards it as a living cell phenomenon, while bleeding of birch and grape he considers to be "without doubt one of root-pressure."

To explain the refilling of cells with water, Münch (115-117) claims that there is a downward stream of water with osmotically active materials in the bark and that when these dissolved materials are removed at the base of the

*See also James and Baker (81) in this connection.

tree, the water is pressed out into the xylem and refills the vessels emptied during the summer. He demonstrated and measured this downward stream by loosening strips of bark from below and collecting the exuded sap, calculating that the translocation stream amounts to about 2½% of the total transpiration stream. Among other things he stresses the very rapid streaming in the sieve tubes as significant. Dixon and Gibbon (35) support Münch, since the osmotic pressure of sap of *Fraxinus excelsior* decreases from above downwards. This would cause water to be forced into the xylem below. Curtis and Scofield (28), however, find a gradient in the reverse direction. Lund (99-101) states that ". . . an electric current flows downward in the outer cortex and upward in the wood axis," and that this introduces ". . . a distinct possibility, namely that one of the functions of the continuous electric current which is directed upward in the wood is to supply electrical energy for electro-endosmotic flow of sap in an upward direction in the conducting vessels of the wood.* This suggestion may also apply to a downward flow in the cortex as well as transport across the stem." The observations of Stamm (163, 165) appear to be in accord with these views.

While the evidence for the tension hypothesis is so overwhelming as practically to negative all other theories of sap ascent, it is possible that the mechanisms of Münch and Lund explain the refilling of the conducting tracts.

The next question is that of the times of such seasonal changes as onset of root pressure, cambial activity and the appearance of tensions in the conducting system. Several facts noted in Europe by Th. Hartig (65-67) are of particular interest in the present discussion, namely that while bleeding in hornbeam, oak, poplar, lime, etc. ceases before the buds open (and in poplar even before swelling of the buds is noticeable) in hawthorn it commences with the bursting of the buds and continues until the leaves are one-third of an inch long, and in the dog-rose bleeding may continue until the young shoots reach a length of 1½ in.

That positive pressures commence to be evident at about the same time as cambial activity begins is well known. But which of the two actually begins first? A review of the literature is not very helpful. Hartig (67) found that cambial activity commenced in the youngest twigs, and Schröder (150) found bleeding to commence and finish in the root! Brown (16) studied forest trees in the United States (Ithaca) and found that in young trees growth commenced somewhat below the apical shoot and spread upwards and downwards, while in older trees it began in the crown. Knudson (89) also noted that xylem growth commenced below the apex of the tree. He found that phloem development proceeded some way before xylem formation began, which was confirmed by Cockerham (22). Knudson distinguished between increase by swelling and actual growth—the former often commencing some time before the latter—an observation which suggests that water movement may occur before much cellular activity is evident. It is difficult to agree with the views of Pearsall and Hanby (124), that growth of leaves is associated

*See also Marinesco (109).

with positive hydrostatic pressures, since negative pressures may be found in poplar before buds open, a fact which is in accord with Th. Hartig's work referred to above.

Observations on bleeding, pressures, tensions and water-contents of *Betula*, *Populus* and *Acer* throw some light on the subject. In Quebec, the maple may bleed freely in the depths of winter, provided relatively high temperatures are reached, but neither poplar nor birch have been seen to do this, though birch may bleed after leaf-fall. At 2 p.m. on March 5, 1932,—a bright, sunny day, thawing a little in the sun—rapid flow was observed from the south side of maple, but none at all from birch or poplar. Large gas bubbles were apparent in the maple sap, and the liquid appeared to flow both from above and from below. On March 29, with a sun temperature of 5.5° C., only maple was bleeding. On April 9, when the air temperature reached 10.5° C. in the sun but the ground was still frozen, only maple was bleeding. On April 16 the ground was still frozen and small patches of snow remained from a recent fall, but maple, poplar and birch were all bleeding freely, the last both at breast height and at 20 ft. from the ground. On May 3 (sun temperature 21° C.), birch continued to bleed a little (maple was not tapped, but commercial tapping was long over). On the same day, however, tensions had become noticeable in poplar, even in trees with no expanding catkins. It was not until May 14, when the birch leaves were about $\frac{1}{4}$ in. long, that tensions in that tree were recorded, and by that time the water content of borings had dropped from 96% (May 3) to 85%.

Why should these three trees, growing together, differ so markedly in their behavior? One possibility is that the maple can absorb water before birch and poplar, and this might be due to a deep root system in the first, extending to below the frozen soil layer. The root systems of two trees were investigated with the following results. A maple (about two feet in diameter) had a very extensive root system, confined almost entirely to the top two feet of the soil, while a birch showed extensive root development in the upper two feet but also had many small roots extending down to four feet below the surface. It is clear from this that the maple had no positional advantage over the birch, as far as drawing water from under the frozen layer was concerned, nor could it have taken water from the upper layers more readily than birch, for the upper layers remained frozen long after bleeding commenced.

Why should bleeding cease and tensions develop in poplar before bud opening and while birch still shows positive pressures? If evaporation from the twigs of the former be much more rapid than that from the latter, then the question might be answered. A few experiments suggest that this is the case, but before describing these it is well to consider the work that has been done on the subject of transpiration from twigs in the leafless condition.

Stephen Hales (63) seems to have recognized that air can pass through the lenticels, and since his time they have been regarded by most botanists as provision for aeration of the massive trunk. Eder (42) studied *Sambucus*

and *Aesculus* in the winter condition and claimed that the lenticels remained open, and Wiesner (201) confirmed Eder's observation that the lenticels of *Sambucus*, at least, are not closed in winter. Haberlandt (62), on the other hand, found lenticels more or less closed during April, May and the first half of June. He carried out some experiments which showed that evaporation from open lenticels is considerable. Stahl (161, 162) recognized two types of lenticels—one with "Lockere Füllzellen und dichtere Zwischenstreifen" (*Betula*, etc.), the other with "Dichtere Füllzellen, keine Zwischenstreifen" (*Populus*, etc.). Klebahn (88) found lenticels open in winter, though they were sometimes a little more permeable in summer, and in particular he states that *Betula alba* (of which the paper birch is a variety) is the same summer and winter. In his extensive monograph on lenticels, Devaux (30) states that "Toutefois une fermeture complète peut exister très souvent non seulement en hiver, mais à toute époque de l'année." He decides that the primary function of lenticels is transpiration and that aeration is a secondary function. Finally, Strausbaugh (170) finds that water loss from plum is correlated with the number of lenticels.

Experiments carried out just before leaf opening (when poplar showed tension and birch still bled), in which air was forced through twigs of the two trees, proved inconclusive, though the lenticels of poplar appeared to be more open than those of birch. In other experiments, short cylinders of twig were waxed in various ways and evaporation was measured by loss in weight. The results (Table II) support the contention that evaporation from poplar is much greater than that from birch at the time of development of the first tensions in poplar. It may be significant too, that poplar logs lose water more rapidly than birch.

TABLE II
EVAPORATION FROM BARK AND LENTICELS OF BIRCH AND POPLAR (MAY 1932)

Species, etc.	Treatment	Evaporation in mg. per sq. cm. per hour in laboratory
Birch, diam. 1.50 cm.	Lenticels waxed, bark exposed	Hardly more than from completely waxed samples
	Lenticels exposed, equivalent area of bark waxed	Hardly more than from completely waxed samples
Birch, diam. 2.75 cm.	Lenticels waxed, bark exposed	0.12
	Lenticels exposed, equivalent area of bark waxed	0.17
Poplar, diam. 1.75 cm.	Lenticels waxed, bark exposed	0.22
	Lenticels exposed, equivalent area of bark waxed	0.33
Poplar, diam. 3.5 cm.	Lenticels waxed, bark exposed	0.27
	Lenticels exposed, equivalent area of bark waxed	0.41

We have seen that bleeding coincides for the most part with time of maximum water content. In the hardwoods a decrease in water content occurs after the leaves open and from 40 to 50% of the volume of the tree may be occupied by gas at the end of the summer. The rapid diurnal changes in moisture content, on the other hand, are not accompanied by corresponding fluctuations in gas content, for high tensions are developed and there can be little doubt that any great increase in gas content would seriously interfere with the rapid uptake of water that undoubtedly occurs. Most investigations of leaf water contents are in complete harmony with this (see Livingston and Brown (97) and Lloyd (98)). Clements and Loftfield (21) found diurnal changes in sap concentration of leaves, which may be correlated in part, at least, with water changes, while Herrick (69) finds that osmotic pressure and suction tension values of *Ambrosia* tend to reach maximum daily values between 1 and 3 p.m.

Hendrickson (68), measuring the effects of irrigation on diurnal changes in water content of *Prunus*, found that leaves, twigs and trunk all showed a similar morning decrease and afternoon increase.* The afternoon increase noted here was also evident in the present work. Observations of stomata of birch revealed the interesting fact that they may close at, or even before, mid-day, and this no doubt means that transpiration is then greatly reduced.

Work on seasonal variation in conifers, summarized in the second paper of this series, shows conclusively that if any variation takes place in these trees (at least in Quebec) it is so small as to defy detection by the strip and disc method. This is not in agreement with the work of Robert Hartig who described marked seasonal changes in conifers growing in Germany, nor of Münch, who gives figures (117) suggesting a loss of 10 to 15% of the total water during the summer. The observations of Haasis on diameter changes of Monterey pine and redwood in California, referred to above, also point to a marked decrease in water content during the summer, but MacDougal, Overton and Smith (104) found no following increase in Monterey pine after the end of the growing season.

Some of the work on comparative transpirations during summer and winter of broad-leaved evergreens, conifers and deciduous trees is pertinent to the present discussion. Mer (111) investigated evergreen leaves under moderately severe climatic conditions, and decided that they carry on some photosynthesis during the winter. The work of Kusano (91) and Miyaké (113) in Japan is in agreement. Water must be carried to the leaves if much assimilation is to proceed. Stahl (161, 162) however, using the cobalt chloride method, concluded that the stomata of evergreens, such as *Buxus*, *Mahonia* and *Taxus baccata* are closed by the end of October, which would imply an almost complete cessation of winter activity. Burgerstein (19) gives the following figures showing the effects of temperature changes on transpiration from *Taxus* twigs in winter: If transpiration is represented as

*Linford, however, finds pineapple leaves thinnest (and driest?) in early morning, and thickest between noon and 4 p.m. (Abstract in Am. J. Botany, 21 : 708-709. 1934).

95 at 12° C., it is 29 at -2° C., 13 at -5.2° and 2 at -10.7° C. Ehlers (43), working with leaves of *Pinus laricio austriaca* in Michigan found leaf temperatures considerably above air temperatures, so that measurements of air temperatures may give an exaggerated idea of the severity of the conditions under which the leaves are functioning. Zacharowa (204), however, registered very small differences for *Pinus sylvestris*—less than 1° C. at an air temperature of about -11° C.—and found that gas exchange of *Pinus sylvestris* and *Picea excelsa* is appreciable at quite low temperatures.

In spite of this far from negligible gas movement, Weaver and Mogensen (196) state that "Winter transpiration losses from conifers are scarcely greater than those from defoliated stems of broad-leaved trees." Iwanoff (80) goes further and maintains that the needles of conifers are better protected against loss of water than are hibernating one-year-old twigs of deciduous trees, while Meyer (112) claims that the leaves of pitch pine do not change in water content during the winter. Von Höhnel (70, 71) gives comparative figures also for the vegetative periods of both evergreen and deciduous trees, and shows that, with the exception of larch which transpires rapidly in summer, the former have only a fraction of the water consumption of the latter. Seasonal figures certainly support the contention that transpiration of conifers does not greatly exceed absorption at any time. Yet another point that fits in with this idea is the general absence of bleeding in the conifers, though MacDougal (102) records slight exudation pressures in *Pinus radiata*.

Movement of Water During Seasoning and Flotation

It is convenient now to consider briefly the problem of sinkage with reference to the results summarized above and in the preceding paper (55). The distribution of wood, water, and gas in some of the species studied is tabulated in Table III, so that some idea of the initial flotability of fresh-cut logs may be obtained.

It is evident from this that flotation of poplar and birch cut in late winter or early spring is impossible without seasoning. The same trees cut in late summer, however, may have average densities as low as 0.69 and 0.77 respectively, giving a good margin of flotation.

In summer-cut birch and poplar, the size of the tree, or the position (top, middle, butt) of the log, will have little influence on the density, for outer rings and inner have virtually the same water content at the end of the summer. If winter-cut, the lower parts—and older trees—of poplar will have a margin over upper and younger material by virtue of the relatively drier, and hence lighter, heartwood.

The flotability of softwoods will not vary with the season of cutting, but it will vary with the size of the tree and the position of the log, since the heartwood is always much drier than the sapwood and is present in relatively greater volume in larger logs. This is true even in the case of balsam, since the characteristic wet patches usually occupy so small a percentage of the heartwood that the average density of that part of the log is almost always well below 1.0.

TABLE III
WATER, WOOD, GAS AND DENSITY OF WOODS, AS CUT IN 1931

Species	Part of tree and time of cutting	Water, % dry wt.	% fresh volume occupied by			Density of fresh wood (water = 1)
			water	wood	gas	
Birch	Outer rings. May-June	>120	>59	33	< 8	>1.10
	Outer rings. July-August	50	24	33	43	0.76
	Whole tree. May-June	97	47	33	20	0.98
	Whole tree. July-August	54	26	33	41	0.77
Poplar	Outer rings. May	>160	>67	27	< 6	>1.10
	Outer rings September	70	29	27	44	0.71
	Heartwood	ca. 70	29	27	44	0.71
	Whole tree. May	125	53	27	20	0.95
	Whole tree. September	66	27	27	46	0.69
Jack pine	Sapwood at all times	170	65	25	10	1.04
	Heartwood at all times	35	13	23	64	0.49
Balsam	Sapwood and wet patches of heartwood at all times	200 to 250	62 to 80	20	0 to 18	0.93 to 1.11

Certain points brought out in the preceding paper may be emphasized here.

1. Water can pass relatively freely through the conducting regions when logs are floated (see Scarth and Gibbs (144)), but passes less readily through the heartwood.
2. The loss of water from a log (unless the bark be removed) occurs chiefly from the ends of the log. This is true also of the re-entrance of water, at least in the early stages, when the log is floated, so that log length is very important and end painting may be effective in maintaining flotability.
3. The rate of entry of water is governed by the rate of solution of gas trapped in the log (see Scarth (143)).
4. The top drying of floated (peeled) logs to well below fibre saturation point proves that movement of water in the walls of the wood, in the radial direction at least, may be the limiting factor under some conditions. This is borne out also by the gradients observed in birch logs seasoned for about a year (Scarth and Gibbs, (144) Fig. 1).

5. The gas mixture in the growing tree contains more carbon dioxide and less oxygen than the atmosphere (104). Fermentation may take place in the seasoning or floating log (11, 12) and this results in a still higher concentration of carbon dioxide (144, Table I). Although the carbon dioxide is more soluble than oxygen—2.8 : 1 at 20° C.—the increased volume delays entrance of water, or may even expel it (11, 12; 55, Fig. 11, log 5A).

6. Insofar as the slow currents set up in the log by top drying might assist in solution and escape of gas, top drying, unless very rapid, might actually be detrimental rather than helpful.

When a dry log is first exposed to water, as Scarth (143) points out, entry both of water vapor and liquid water takes place. The cell walls are soon saturated—as volume measurements show—and the air in the cell cavities becomes laden with vapor. After this state has been reached, further entry involves displacement or solution of the air by liquid water. Solution is very gradual; or rather, the diffusion of the dissolved gas is so slow that solution itself is slowed down. It is fortunate for the floater of logs that this is so, since penetration is hindered thereby. But when the matter is approached from the point of view of the mill-men, this solution must be replaced by displacement if even and quick penetration of cooking liquors, etc. is to be attained.

In all these considerations the problem of the passage of water and gas from cell to cell is of the utmost importance, just as it is in the ascent of water in the tree. The difficulty of reconciling the comparatively easy passage of air through bordered pits with the maintenance of water tracts under high tensions has been emphasized above. It crops up again here when measurements of penetrability are made.

Mass flow of water in narrow tubes and in the walls of the cells is fairly well understood, but the question is greatly complicated when air is present. It is possible from observation of the pressures necessary to displace air, and from the permeability of walls to "solutions" containing particles of known size, to get some idea of the diameter of the pores in the walls and pit membranes. The work of Stamm and Bailey has already received notice in this connection. Pore size has been calculated also by Renner (137) and by Frenzel (50). The formula employed is a relatively simple one—used in the calculation of capillary rise in narrow tubes—and substitutes pore radius for tube radius and the pressure necessary to overcome the resistance in the pore (expressed in terms of hydrostatic pressure) for the rise of liquid. We

have: $h = \frac{2\gamma}{rsg}$, where h = pressure (expressed as cm. of water), γ = capillary const. = 77 ergs, r = radius of pore in cm., s = density of water = 1, g = 981 dynes. From this it may readily be shown that the pores in the pit membrane are of the order of 0.5–1.0 μ (requiring 3–6 atm. for the displacement of air), while the "intermicellar spaces" of the walls are very much smaller. (Frenzel calculated that the latter are of the order of 1 $\mu\mu$, requiring a pressure of 3000 atm. to force air as such through them.) The contention of Renner,

that the springing of the fern annulus at tensions of about 300 atm. demands a pore diameter of about $10 \mu\mu$ is surely not justified, for air in solution might pass through at much lower pressures and come out of solution at 300 atm. It is not necessary to postulate mass movement of air as such through the walls in this case. It is thus evident that pore diameter in wood sets a lower limit to the pressures necessary to produce displacement of air. Two obvious steps present themselves at this point if increased penetration be desired: (a) Utilization of the natural permeability of wood to the fullest advantage, and (b) use of some means to increase effective pore diameter. The first step involves the selection of optimum chip size and shape in mill practice, the second the treatment of the material by physical or chemical means. As a preliminary to (a), Saunderson (142) describes the "worst possible" chip shape for sprucewood! The improvement of penetrability under (b) may result from an actual increase of pore diameter or from other changes that render effective pores already present but not available for penetration. Little is known of the first possibility, though Sutherland (172) believes that rate of penetration of balsam and red pine, which increases more rapidly with pressure than one would expect, is due to bulging of the pit membranes and consequent increase in pore diameter. The second involves the freeing of adhering tori in heartwood, and need not be discussed here as it has received attention in the first paper of this series (54).

A point of some importance is the curious behavior of sapwood noted by Scarth (unpublished work). When water is forced by ordinary tap pressure in a longitudinal direction through a block, an initial very rapid flow is obtained which falls off after a few minutes. When direction of flow is reversed, it is again rapid, and once more falls away. This might be due to torus action or to blockage of the pores by particles of some sort. Johnston and Maass (85) and Sutherland (172) claim never to have observed torus action in their studies on jack-pine, spruce, etc. but their experiments do not include application of high pressure to sapwood. The observations of Frenzel (50) on the blocking of pits by colloidal gold particles may be an analogous phenomenon—though he makes the curious claim that the particles clog the pits between torus and border on the side away from the pressure. Sutherland (172), who observed similar cessation of flow, thinks it may be due to "Jamin chain" formation.

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A MACHINE FOR TESTING THE RESISTANCE OF PLANTS TO INJURY BY ATMOSPHERIC DROUGHT¹

BY O. S. AAMODT²

Abstract

This machine consists of a glass chamber with a capacity of 40-50 six inch pots through which is forced air which has been heated by thermostatically controlled electric heaters. Dampers and baffles are provided to control the flow of air and to reduce eddies. After exposure for 8-15 hr. at 110° F., 14% relative humidity, and an air velocity of six miles per hour, wheat varieties known to be drought resistant in the field showed less injury from drought than varieties known to be non drought-resistant.

The success of crop improvement programs is usually judged by the degree to which yield and quality have been modified. The pure line theory made it apparent that crops could not be continually improved by selection within a given variety. Elaborate yield tests have resulted in the elimination of varieties markedly affected by certain factors, and the retention of others less affected by these factors. The preferred varieties are not always retained because they possess similar desirable characteristics. The defects in one may be compensated for by desirable characters lacking in others. Information is needed as to why certain varieties perform more satisfactorily than others.

At the beginning of the present century Mendelian methods were introduced generally into the improvement of cereal crops. The mode of inheritance of characters that are readily observable, such as awns, seed color, plant height, maturity, etc., was studied intensively. In many instances simple Mendelian ratios were found. In some cases complicated segregations were obtained and the inheritance of the characters in question was designated as being due to numerous, multiple or probably modifying genes. These early studies, and many present day studies of the same nature, demonstrate that Mendelian principles can be applied to inheritance in cereals, and that a genetic mode of attack is the proper basis for sound crop improvement. Until recent years, however, breeding projects have ignored some of the more pertinent problems in successful crop production. We are sadly lacking in exact information on the mode of inheritance of such important characters as drought resistance, quality, straw strength, winter hardiness, resistance to disease and insect pests, etc. These are the characters that influence directly both yield and quality.

Instead of selecting or breeding for such complex characteristics as yield and quality, it would be more effective to determine the characteristics upon which yield and quality depend. High yield is a character which can be

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determined accurately only over a long period of years. It is not finally determined until the variety has been exposed to all the unfavorable conditions which are likely to occur in the region in which it is to be grown. Fundamental studies on the factors that influence yield are greatly needed. Susceptibility to disease and lack of drought or winter hardiness are recognized as having a direct effect on yield, but the mode of inheritance of the plant's reaction to disease, drought and low temperatures unfortunately is not well known. Knowledge concerning these factors has been limited because of the failure to reproduce them artificially and have them act in a differential manner on the plants being studied. The development of low temperature chambers, artificial disease epidemics, etc., has aided materially in obtaining the desired information. These special methods have contributed greatly to our knowledge of what is wanted in the way of specific and definite varietal characteristics. They have been of great practical value in shortening the period of test required to determine the degree to which a given variety possesses a certain character. Knowledge of why certain varieties perform better than others is of primary importance to the plant breeder. Rapid progress is taking place in the development of laboratory and plot technique for studying the important characters concerned with yield and quality, and in methods of combining the desired characters into a single variety.

A project on breeding for drought resistance in spring wheat was initiated at the University of Alberta in 1929. Soil moisture at Edmonton, Alberta, in most years is sufficient to provide for normal growth and good average yields of grain. Droughts are infrequent, and usually of short duration. Under these conditions there is little opportunity for selecting plants resistant to drought from the segregating hybrid populations. It was evident that either the work must be carried on in a region in which moisture is more of a limiting factor in crop production than it is at Edmonton, or special equipment and laboratory technique would have to be developed for determining artificially the inherent ability of varieties and hybrids to grow and produce grain under conditions of limited moisture.

It is generally recognized that there are two kinds of drought, namely, soil and atmospheric. Soil drought prevails when the soil ceases to provide the plant with sufficient water to take the place of that lost by the leaves in transpiration. The methods for testing plants for differences in ability to withstand soil drought are comparatively simple. Atmospheric drought is caused by hot dry winds which may produce desiccation and killing of the plant tissues even when soil moisture is relatively plentiful. Soil drought is more injurious to the plant, but a combination of both kinds of drought is disastrous. Resistance to drought is usually defined as the capacity of the plant to endure wilting.

A brief description of a special machine for producing artificial drought conditions was received in correspondence with Dr. T. Maximov of the Institute

of Applied Botany and Plant Breeding, Leningrad, Russia, in 1932. The machine was developed for the purpose of testing plants for resistance to "windburn". "The whole thing consists of a glass cage in the middle of which is placed a round table with six holes for pots with plants that turn around on an axis, to allow the plants to have uniform conditions of wind that is blown in with the help of a strong ventilator (fan). Before the air comes into the cage it is heated by means of an oven (they can be of different sort—electrical or heated with oil or wood), which under certain outside conditions very often is sufficient to make it about 16-18% of humidity when it reaches the chamber. Sometimes we also applied an additional drying of the air by means of CaCl_2 or by a cold water stream. The wind velocity in our experiment was usually 3 meters per second which, with a temperature of 37-39° C. was just what we needed to provoke an artificial windburn".

The construction of a drought machine with a rotating table, similar to the Russian one, would give a very limited capacity for plant material. In order to be of any great practical value in testing the numerous hybrid strains produced by the plant breeder, the machine should have a capacity of 40-50 six inch pots. A study of the climatic conditions prevalent in the dry area of Alberta during periods when the wheat plants are severely injured by drought indicated that the machine should be able to produce the following conditions: (a) a temperature of 100-120° F.; (b) a wind velocity of 3-10 miles per hour; and (c) a relative humidity of 10-20%. A preliminary report on the construction of the machine was made in 1933 (1).

The type of wind chamber finally decided upon was a glass tunnel 30 in. wide, 10 ft. long, and 40 in. high (Fig. 1). Glass was used in the construction of the chamber in order to provide light conditions as near as possible to normal. One end of the glass chamber was connected by a covered galvanized iron tunnel 20 in. in diameter to the heating units which were placed beneath the floor of the glass tunnel (Fig. 2).

A No. 5 Ventura fan was installed where the glass and galvanized iron tunnels joined. When in operation the fan drew the hot air from the heating units and blew it out through the glass tunnel. It would be undesirable to have the fan motor operating at the high temperature in the tunnel, consequently the short shaft connecting the motor and fan was replaced with one 4 ft. in length. This brought the motor end of the shaft outside the tunnel where it was connected by a pulley and belt drive to the motor (Fig. 2).

With a high air flow it would be impracticable to produce all the heat required with electrical heating units. The machine (which was nicknamed the "chinook" machine) was set up in the greenhouse where the air which was drawn into the electrical heaters could be conditioned easily and cheaply with the regular greenhouse steam heating units. Eight electrical heater coils were made of 16 gauge Nichrome IV heating wire and mounted on

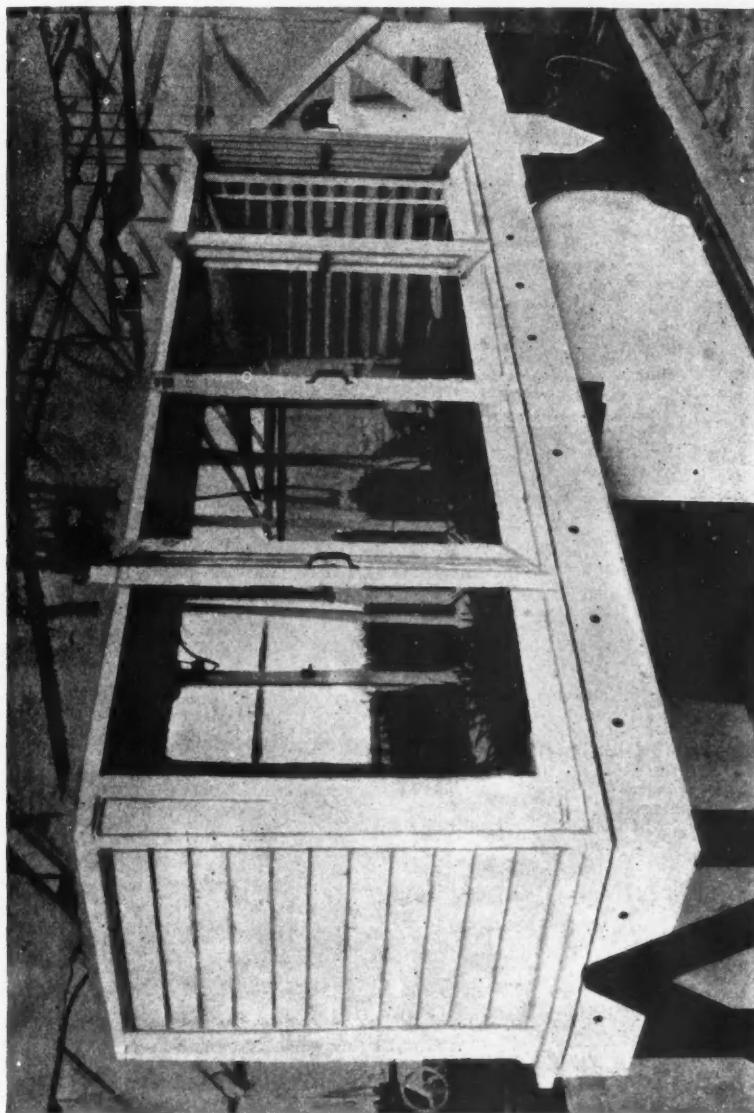


FIG. 1. Front view of the chinook machine showing the glass tunnel with baffle plates in front of the fan and at the end of the tunnel. Air intake and chamber containing electric heating coils shown underneath glass tunnel. Floor of the tunnel shows pots submerged below the path of the hot winds in moist cool sand.



FIG. 2. Rear view of the Chinook machine showing the curved wind tunnel connecting the electrical heating units below to the glass tunnel above. Fan motor is placed outside heating tunnel with four-foot drive shaft and pulley with belt.

Transite panels, as shown in Fig. 3. These were placed in a well insulated chamber at the end of the galvanized iron tunnel underneath the glass tunnel. Each of six of the heaters was composed of 50 ft. of wire and each of the two control heaters, of 100 ft. of wire. The coils were arranged so that they could be connected either in series or parallel. The heaters are controlled by four externally operated switches, shown on the side of the machine in Fig. 2. A deKhotinsky bimetallic thermoregulator was placed in the glass tunnel directly in the path of the air flow to give automatic control of the air temperature.

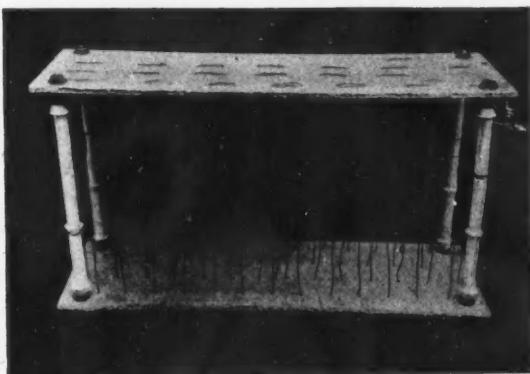


FIG. 3. One of the electrical heating units consisting of 50 ft. of 16 gauge Nichrome IV heating wire drawn through Transite.

The air flow was controlled by sliding doors at the opening, or air intake end, of the electrical heating chamber, and also by the baffles placed at both ends of the glass tunnel (Fig. 1). The wind velocity was regulated readily within limits at any desired speed by adjusting the sliding doors and baffles, thus causing a greater or less resistance to the flow of air. In the preliminary tests it was discovered that there were several air eddies in the glass tunnel. Small eddies were found in the four corners of the tunnel next to the fan while a large one, about a foot in diameter, extended from the centre of the fan, and tapered off at a point six feet out. A set of baffles placed in front of the fan (Fig. 1) broke up these eddies. This improvement, while causing a reduction of about three miles per hour wind velocity, greatly improved the uniformity of wind distribution in the tunnel. The draw shutters at the exit end of the glass tunnel were also replaced by a set of baffles. Being adjustable they aided considerably in the regulation of the temperature of the air currents.

At first some difficulty was experienced in maintaining a constant temperature of 112° F. for an eight hour period. Three factors were found to be very important in controlling the temperature of the wind passing through the tunnel, *viz.*, the temperature of the greenhouse, the size of the wind inlet aperture, and the size of the outlet aperture. After a few trials it was found that when the temperature of the greenhouse was approximately 85° F., the heating units were able to control the temperature of the tunnel between 110-112° F. for an indefinite period.

Studies were immediately begun on the reaction to atmospheric drought of several drought resistant and non drought-resistant varieties of wheat, which were used as parents in the breeding program. Marked differences were noted in the reaction of these varieties to atmospheric drought (Fig. 4). As soon as a routine technique was worked out, a number of F_4 hybrid lines were exposed, and they likewise showed marked differences in their abilities to withstand injury from atmospheric drought. Resistance to artificially produced atmospheric drought of Milturum 0.321 (drought-resistant), and Selection I-28-60 (non drought-resistant), together with five F_4 hybrid lines,



FIG. 4. Reaction to atmospheric drought of parental varieties and hybrids of a cross between Milturum (drought-resistant) and Selection I-28-60 (non-drought-resistant). Exposure 15 hr. at a temperature of 110° F., 14% relative humidity and wind velocity 6 m.p.h. Back row: Two pots on left, Milturum. Two pots on right, I-28-60. Front row: Five F_4 hybrid lines. All dead tissue was removed before photographing.

is shown in Fig. 4. These preliminary results indicated that the chinook machine would be of considerable value in differentiating between varieties and hybrids resistant and non-resistant to atmospheric drought. An intensive study of the whole problem has been undertaken. Results obtained in the laboratory with artificial conditions were checked by growing the material under natural drought conditions in the field. The field experiments are conducted in the drought area at Brooks, in the southeastern part of the province. The details of the experiments conducted, and the results obtained in the laboratory, are being reported in a separate paper by Aamodt and Johnston (2), and the field studies by Aamodt and Torrie (3) and Torrie (4).

Acknowledgments

The writer gratefully acknowledges the valuable advice given by Dr. W. H. Cook in designing the machine, and the able assistance of R. G. Brewer and W. Jullyan in its construction; also the encouraging support received from Dr. R. Newton in the whole investigation.

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A GRAPHICAL STUDY OF THE BLOOD OF NORMAL FOXES¹By ARNOLD H. KENNEDY²

Abstract

The fluctuations and trends of various cellular elements of normal fox blood are presented in graphical form. The graphs have been prepared from data obtained from a number of foxes of various ages and show the minimum, maximum and mean numbers of blood elements occurring in both males and females in each age group.

The red blood cells, haemoglobin, and to a lesser extent the neutrophiles, on the one hand, have trends of a similar nature and appear to be related. On the other hand the total white blood cells, lymphocytes, monocytes and basophiles also appear to be closely related. A comprehensive picture of the field tends to divide the numbers of blood elements composing the blood of foxes into these two divisions.

The trends and fluctuations, for the same age groups, of the total white blood cells and lymphocytes are almost identical. The monocytes and basophiles also show close similarity. A close similarity in general trend, with less marked fluctuations, exists in the four groups, total white blood cells, lymphocytes, monocytes and basophiles.

Introduction

In order to present the fluctuations and trends of the various cellular elements of normal fox blood, graphs have been prepared. These graphs, based on data from foxes of various ages, are presented in this paper.

Although it is fully appreciated that blood examinations made from a group of foxes, of nearly the same age, and bled at regular intervals, would give a more regular and uniform graph, it was thought that more useful comparative information on the trends of numbers of blood elements could be obtained from blood examinations of healthy, normal foxes grouped according to age.

For this work silver black foxes were divided into groups, according to sex and age. The age groups range from under one month to four years of age and over. An examination was made from each fox in the groups. Each group contained approximately ten male and ten female foxes. Any variation in the cell count in the different age groups was noted and recorded. The maximum, mean and minimum numbers of the various blood elements were determined for each group, and graphs prepared from the data obtained. Some irregular variations due to the effects of chance sampling may be shown in some of the graphs. The standard deviation for the foxes in each age group (Tables I and II) was determined in order that any significant differences between age groups might be noted.

The graphs show at a glance the trend of each blood element throughout the life of a fox.

According to Kennedy (1) the eosinophile is not found in fox blood, but is replaced by a cell which is distinctly basophilic in staining reaction and which is classified as a basophile.

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Contribution from the Ontario Government Experimental Fur Farm, Kirkfield, Ontario.

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Methods and Technique

Extraction of Blood

The fur was clipped from the integument between two toes and the area cleaned with alcohol, thus exposing the blood vessel located in this region. The vessel was then pricked with the sharp point of a No. 11, Bard Parker scalpel. The first few drops of blood were rejected and then samples were drawn into the pipettes. Standardized pipettes and haemocytometer were used for estimating the cell counts. For the haemoglobin readings, a Sahli haemoglobinometer was used. For the differential count of the leucocytes the blood smears were stained with Hasting's stain and two hundred cells were differentiated under the oil immersion lens.

The Graphs

Figs. 1 to 9 were prepared from the minimum, maximum, and mean numbers of blood elements occurring in both males and females in each age group of foxes. A solid black line was used to designate the numbers of blood elements in males and a broken or interrupted line the numbers in female foxes. The trends or changes occurring over long periods, and the fluctuations, showing the short-period changes, indicate at a glance any increase or decrease, rapid or gradual, that may occur in the number of blood elements at the different stages in the life of the fox. A review of the curves collectively demonstrates the relations of the numbers of the blood elements to one another. Some sets of groups appear to be very closely related while others do not appear to be related.

The standard deviation has been calculated by dividing the sum of the squares of the deviations from the mean by the numbers of cases recorded, and taking the square root of the result. The standard deviations for the foxes comprising each age group are shown in Tables I and II.

TABLE I

STANDARD DEVIATION OF NUMBERS OF RED BLOOD CELLS, GRAMS OF HAEMOGLOBIN, AND COLOR INDEX FOR THE FOXES COMPRISING EACH AGE GROUP

Males				Females			
Age	R.b. cs.	Hb., gm.	Index	Age	R.b. cs.	Hb., gm.	Index
Months				Months			
0- 1	±1.072	±0.65	±0.01	0- 1	±0.825	±0.66	±0.07
1- 2	±0.686	±0.67	±0.07	1- 2	±0.665	±0.53	±0.04
2- 3	±0.636	±0.77	±0.05	2- 3	±0.694	±1.52	±0.09
3- 4	±0.498	±0.38	±0.01	3- 4	±0.753	±0.33	±0.03
4- 6	±1.108	±1.08	±0.03	4- 6	±0.604	±0.76	±0.04
6- 8	±0.977	±0.75	±0.07	6- 8	±0.783	±1.40	±0.06
8-10	±0.492	±0.75	±0.05	8-10	±0.475	±1.05	±0.05
10-12	±1.009	±1.05	±0.05	10-12	±0.832	±0.55	±0.05
12-19	±0.973	±1.19	±0.06	12-19	±1.118	±0.65	±0.07
Years				Years			
2- 3	±1.082	±2.27	±0.08	2- 3	±0.939	±1.50	±0.07
3- 4	±1.308	±1.05	±0.06	3- 4	±1.421	±1.09	±0.05
4- 5	±0.494	±0.41	±0.02	4- 5	±0.483	±1.28	±0.08
				Aged	±0.948	±1.55	±0.07

TABLE II

STANDARD DEVIATION OF THE LYMPHOCYTE, MONOCYTE, NEUTROPHILE AND BASOPHILE COUNTS OF THE FOXES COMPRISING EACH AGE GROUP

Males					Females				
Age	Ly.	Mo.	Ne.	Ba.	Age	Ly.	Mo.	Ne.	Ba.
Months					Months				
0- 1	± 738	± 142	± 1679	± 461	0- 1	± 693	± 67	± 1338	± 387
1- 2	± 1258	± 135	± 1312	± 141	1- 2	± 1376	± 138	± 2090	± 228
2- 3	± 1995	± 157	± 1111	± 276	2- 3	± 1127	± 91	± 654	± 161
3- 4	± 1565	± 149	± 1545	± 503	3- 4	± 1611	± 115	± 1474	± 394
4- 6	± 1758	± 187	± 1825	± 211	4- 6	± 2063	± 162	± 1733	± 336
6- 8	± 1198	± 271	± 1483	± 690	6- 8	± 1256	± 252	± 1079	± 224
8-10	± 1117	± 97	± 852	± 279	8-10	± 904	± 111	± 1846	± 201
10-12	± 762	± 144	± 145	± 224	10-12	± 936	± 58	± 2032	± 158
12-19	± 1629	± 189	± 1388	± 904	12-19	± 1662	± 142	± 1967	± 383
Years					Years				
2- 3	± 1592	± 75	± 2912	± 219	2- 3	± 1168	± 171	± 2520	± 491
3- 4	± 1850	± 139	± 2082	± 331	3- 4	± 1935	± 67	± 1457	± 340
4- 5	± 564	± 88	± 541	± 1297	4- 5	± 708	± 286	± 1842	± 648
					Aged	± 1102	± 94	± 1052	± 194

Fig. 1. Red Blood Cells

The red blood corpuscles vary from month to month in animals of all ages. A steady increase in the numbers of red blood cells was shown in both the male and female fox pups until the age of four to six months. After this age the average increase was not so marked but a slight upward trend continued

until the foxes were between ten and twelve months old. After twelve months of age, both male and female foxes showed a reduction in the numbers of red blood cells per cu. mm. A diminution in the average numbers of red blood cells per cu. mm. of blood appears to take place in both male and female foxes as they mature.

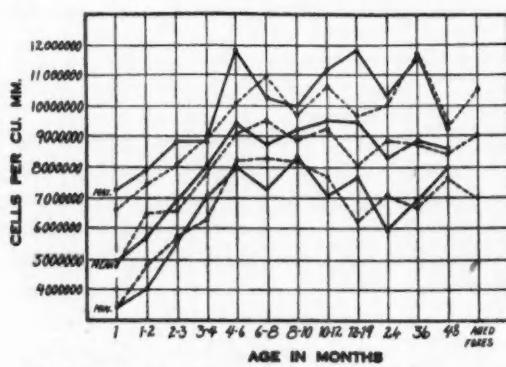


FIG. 1. Red blood cells. Males —. Females - - -.

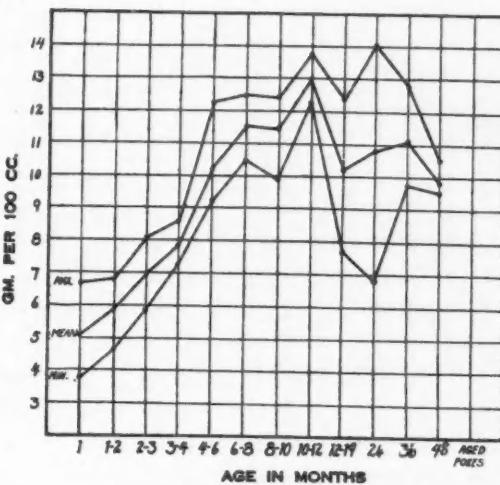
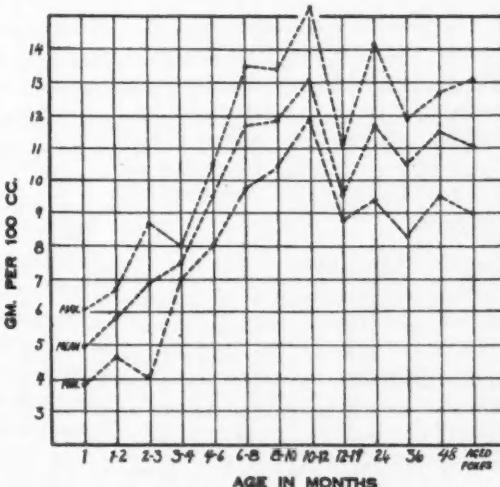
Figs. 2 and 3. Haemoglobin

Because of the fact that the trends for haemoglobin in the males and the females were so similar, it was found necessary to chart them separately to avoid confusion.

The haemoglobin shows a very marked relation to, and follows very closely, the trends of the red blood cells when the groups are taken as a whole. This is particularly evident in the striking similarity of the haemoglobin curves for the females, although these have greater fluctuations. The amounts of haemoglobin increased with age in both the male and female groups up to ten to twelve months of age. In foxes six to ten months of age, very little increase in the haemoglobin occurred. After this age a rapid increase again took place. A rapid fall in haemoglobin occurred between twelve and nineteen months of age. After this age the haemoglobin increased but decreased again in the adult males at four years of age. As the adult foxes increased in age the haemoglobin in the blood decreased.

Fig. 4. Color Index

From under one month of age to between three and four months the color index showed a decline, after which it increased. The highest index reached was found in foxes ten to twelve months old. After this age the index decreased with advance of age of the foxes.

FIG. 2. *Haemoglobin. Males only.*FIG. 3. *Haemoglobin. Females only.*

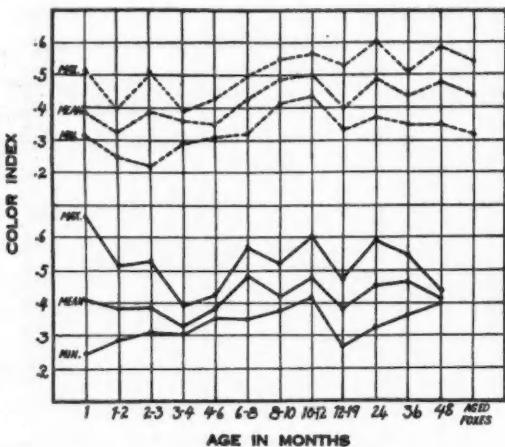


FIG. 4. *Color index. Males* —. *Females* - - -.

in numbers up to the age of four to six months, commenced to decrease rather rapidly. The decrease continued in the females to the age of eight to ten months and in the males continued to the age of ten to twelve months. The lymphocytes commenced to decrease in the females at an earlier age than in the males and also reached the low level at approximately two months earlier than in the males. After reaching the low level the lymphocytes again showed a rapid increase in numbers, reaching a peak in both males and females between the ages of twelve and nineteen months. From this age on, the lymphocytes decreased in numbers.

Fig. 7. *Monocytes*

The average number of monocytes per cu. mm. shows very little variation in the groups from young pups to adult foxes. A slight increase occurred in the males between four and six months of age. The highest number reached in the female foxes occurred between six and eight months of age which was a month later than in the males. The numbers decreased in the males between the ages of eight and ten months after which there was a gradual increase in the average number until four years of age. In

Fig. 5. *White Blood Cells*

The white blood cells show a steady increase up to six months of age, after which a decrease in the numbers takes place. A low level is reached in the females between eight and ten months of age and in the males between ten and twelve months of age. In adult foxes the numbers of white blood cells tended to increase.

Fig. 6. *Lymphocytes*

The lymphocyte cells showed a steady increase up to six months of age, after which the numbers decreased. The decrease continued in the females to the age of eight to ten months and in the males continued to the age of ten to twelve months. The lymphocytes commenced to decrease in the females at an earlier age than in the males and also reached the low level at approximately two months earlier than in the males. After reaching the low level the lymphocytes again showed a rapid increase in numbers, reaching a peak in both males and females between the ages of twelve and nineteen months. From this age on, the lymphocytes decreased in numbers.

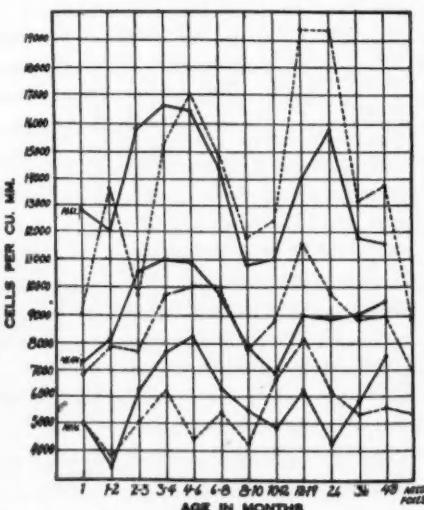


FIG. 5. *White blood cells. Males* —. *Females* - - -.

the females a decrease occurred between the ages of ten and twelve months after which the numbers increased to two years of age. There was a decrease at three, and an increase at four years of age.

Fig. 8. Neutrophiles

The neutrophiles show a relation to the red blood cells. The trend of the neutrophiles does not reach any marked peaks or low levels. There is an upward trend until between three and four months of age. From this age up to between two and three years in both the male and female groups the average neutrophile numbers remained practically at the same level, with a tendency towards a slight increase. The numbers fluctuate slightly above or below 4,500 per cu. mm. After this age the numbers decrease slightly, especially in the female.

Fig. 9. Basophiles

The male foxes showed a decrease in numbers of basophiles at the age of one to two months, after which the number increased. The females continued to show a decrease to the ages between two and three months. In female foxes between four and six months of age an increase in numbers

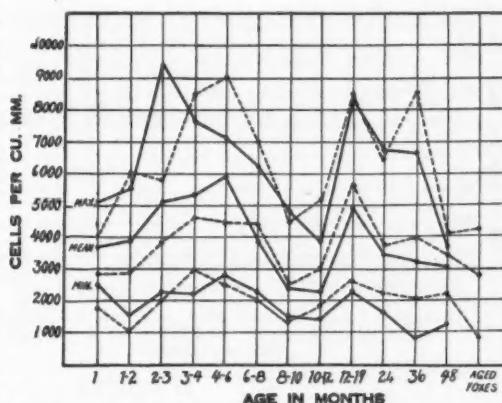


FIG. 6. Lymphocytes. Males ——. Females - - -.

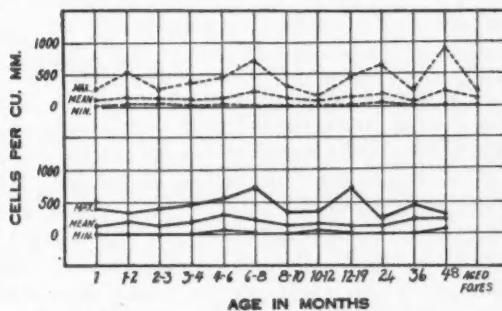


FIG. 7. Monocytes. Males ——. Females - - -.

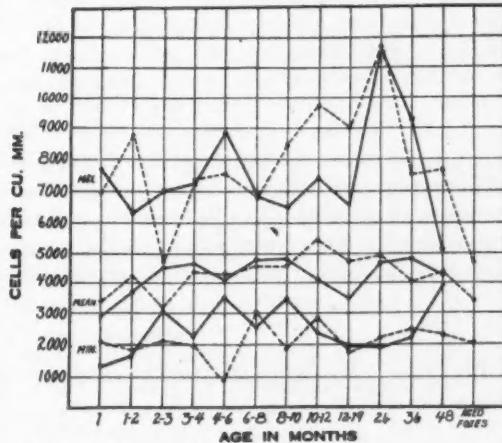


FIG. 8. Neutrophiles. Males ——. Females - - -.

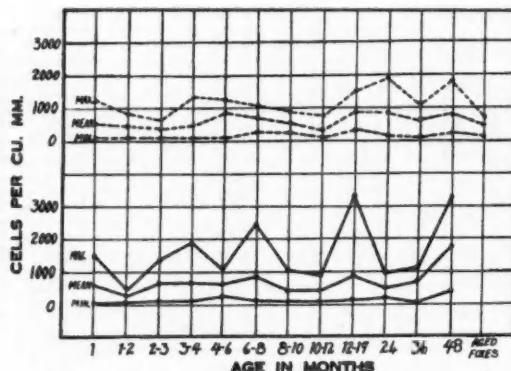


FIG. 9. *Basophiles. Males* —. *Females* - - -.

months of age, after which a gradual increase, with slight fluctuations, continued to the age of three years. A marked increase is shown at four years of age.

Discussion

The red blood cells, haemoglobin and to a lesser extent the neutrophiles, on the one hand, have similar trends and appear to be related. The total white blood cells, lymphocytes, monocytes and basophiles, on the other hand, appear to be closely and intimately related. A comprehensive picture of the data collected tends to divide the numbers of elements composing the blood of foxes into these two divisions. Figs. 4 and 5 show that the total numbers of white blood cells and lymphocytes are almost identical in trends and fluctuations for the same age groups, as are also the monocytes and basophiles as indicated by Figs. 6 and 8. Again a close similarity in general trend with less marked fluctuations exists among the four groups, total white blood cells, lymphocytes, monocytes and basophiles. A general observation of their curves shows two well defined peaks divided by a marked depression occurring in foxes eight to twelve months of age. The peaks and depressions are very marked in the total white blood cell and lymphocyte curves and less prominent in the monocyte and basophile curves. In the foxes between eight and twelve months of age the haemoglobin, red blood cells, and to a slight extent the neutrophiles are numerically inversely related to the total numbers of white blood cells, lymphocytes, monocytes and basophiles. The curves for the first group mount to their highest points at eight to twelve months, while those for the other types of cells descend.

Reference

1. KENNEDY, A. H. Studies on the normal blood of foxes. Ontario Department of Game and Fisheries Bulletin No. 6. Toronto. 1933.

occurred. This was followed by a gradual decrease until ten to twelve months of age was reached. The decrease was followed by an increase in numbers, with slight fluctuations, to the age of four years. In the male foxes between six and eight months of age the average numbers for the group increased. A slight decrease occurred in the average for the group between eight to ten months of age, after which a gradual increase, with slight fluctuations, continued to the age of three years. A marked increase is shown at four years of age.

NOTE ON THE VARIATIONS IN AREA AND IN STAINING
INTENSITY OF RED BLOOD CELLS AND ON
THEIR CORRELATION¹

BY ALFRED SAVAGE², C. H. GOULDEN³ AND J. M. ISA⁴

Abstract

By means of a laborious technique, based on the use of a projection microscope and a sensitive electric photometer, it has been shown that both the areas and transparencies of stained red blood cells may be determined. From the few observations completed, it appears that, statistically, these attributes are positively correlated in normal human blood and their regression line is straight. In pernicious anemia the A/T correlation is negative. Cases of secondary anemia may show either positive or negative A/T correlations. The pathological blood specimens studied all showed non-linear A/T regression lines.

Introduction

In 1931 Savage and Isa (6) reported upon the deflections produced when highly magnified images of red blood cells, stained with acid fuchsine, were projected one at a time into a suitable electric photometer. They demonstrated that, when a series of images were dealt with statistically, the deflections exhibited a greater degree of variation than that shown by the estimated areas of a comparable series. The disagreement was very evident in the case of blood films prepared from anemic patients. By way of explanation, the writers indicated (a) that the images of red blood cells in any series differed visibly in staining intensity as well as in size, (b) that these attributes jointly affected the photometer and (c) that the number of combinations of them which seemed possible would include a wide range. No attempt was made, however, to separate these two attributes.

Scope

This paper describes a method whereby it has been possible to separate and correlate the variations in size and staining intensity of red blood cells. It deals with these properties in the case of normal human blood and touches on them in certain pathological conditions.

General Procedure

The method consisted, essentially, of taking two different observations on each red blood cell of a series. One of these, obtained directly, indicated the area-staining intensity complex. The other was indirect and showed only the area. From these the transparency was derived arithmetically. Figures representing the transparencies and the areas of all the cells in a series were then correlated and subjected to statistical analysis.

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Apparatus

The projection microscope and illuminant were those described elsewhere (6, 7), with the addition of a "Watson-Conrady" auxiliary substage condenser. To ensure steadiness, the light was operated by current from a large battery of accumulators and controlled by a suitable rheostat.

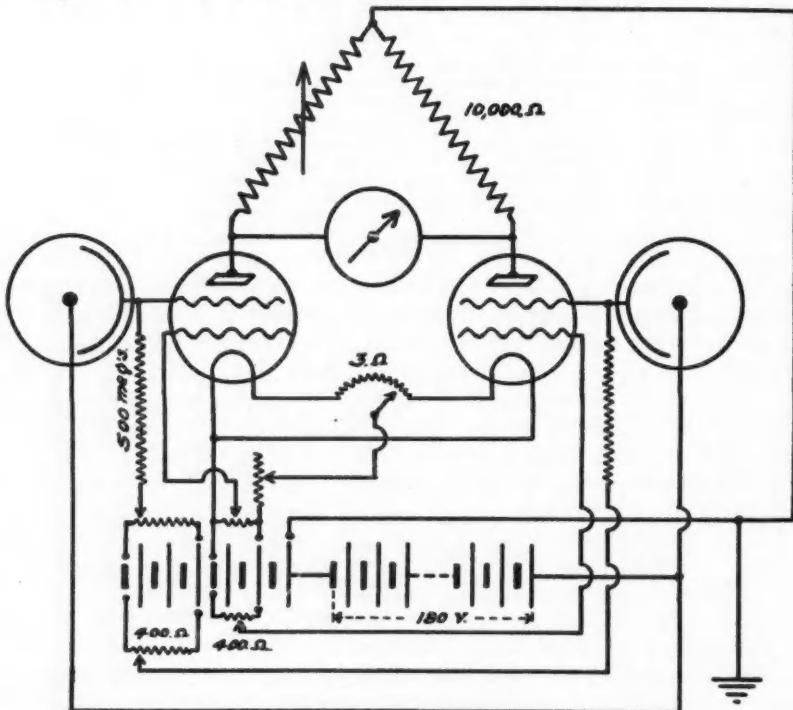


FIG. 1. *The photometer circuit.*

Fig. 1 indicates the photometer circuit. Fundamentally, this was the bridge arrangement devised by Wynne-Williams (8) and modified by DuBridge (2) to suit the FP-54 vacuum tubes of Metcalf and Thompson (3). Both the Burt cells and the valves were very closely matched in all particulars.

By using grid leak resistances of 1000 megohms and a nitrogen filled, tungsten filament lamp there was obtained a calculated galvanometer response of approximately 7000 cm. per lumen. The arrangement was practically free from "drift".

The projection screen was perforated by two circular openings, 2 in. in diameter and 6 in. apart, each of which led to one of the photo cells. They were referred to as the measuring eye and the balancing eye. Between them and perpendicular to the projection surface, an opaque, dull, black screen was erected in such a way that variations in the light admitted to one of the cells was without effect on the other.

Methods

(1) Fixation and Staining of Slides

Having been prepared as thinly as possible in the usual way, the blood films were fixed in absolute methyl alcohol. They were stained in a saturated aqueous solution of acid fuchsin and then washed until no stain could be seen in the plasma between the corpuscles. Rapid drying in air followed.

Unfortunately, because of an exacting prerequisite for this work, namely, that an adequate number of the cells must be quite widely separated, it was not possible to make use of some valuable slides with which the writers had been furnished.

(2) Use of Photometer and Microscope

All the circuits were closed for at least one hour before observations began. This permitted the warming of apparatus indicated elsewhere (7) as necessary. With the photo cells in darkness, the bridge amplifier was then balanced according to the general procedure of Barker and Belchett (1).

Following this, light was admitted to the measuring eye through the projection microscope (blank field) and an equal amount of light *from the same source* was reflected by a mirror into the balancing eye. This beam did not pass through the microscope: its regulation by a diaphragm afforded a convenient and delicate means of keeping the photometer balanced when illuminated.

Throughout observations the light was adjusted so that the galvanometer response was 150 ($\pm 2.$) mm. for that portion of each blank field which entered the measuring eye.

(3) Measurements of Area and Transparency

a. The area-staining intensity complex. An image of a red blood cell, at 3000 diameters magnification, was focused on the projection screen immediately above the measuring eye. Here its outline was carefully drawn in pencil on a piece of thin, white Bristol board, 2 \times 3 in. The photometer, having been balanced and checked, the image was then moved into the eye and the galvanometer deflection written (in red) on the card beneath the cell outline.

This was repeated until 400 images (and cards) had been dealt with. The procedure was very tiresome and required from seven to nine hours of careful team work on the part of two observers. It should be almost needless to add that the darkroom was not lighted during this performance except by the small, carefully shielded lamp, necessary for writing.

b. Area. To render them opaque, the cards were subsequently painted a dull black on the sides which contained no data. Then, the outlines were carefully cut out with scissors and, for safe-keeping, each was placed between the pages of a book, together with the stub of the card from which it came.

The comparative areas of the "silhouettes" were obtained by moistening each one slightly and placing it against the glass plate which covered the measuring eye. There it adhered and, because the light conditions were the

same as those which were maintained during the observation of stained cells, the resulting deflection indicated the area of the corpuscle at the magnification employed. As in the previous series of observations, the galvanometer deflections were written on the card stubs but this time *black* ink was used to avoid possibility of confusion.

This part of the work was comparatively rapid. A series of 400 areas could be measured quite easily in three hours.

c. Staining intensity; transparency. The red figure on each card divided by the black one indicated the amount of light which the stained image had cut off, in other words, its average opacity or staining intensity. Conversely, the difference between the black and red figures, divided by the former, showed the average transparency of the image. It is evident that, when added together, these two values equalled unity.

While this form of expression had to suffice for statistical purposes, it was not ideal in that it ignored the manner in which the stainable material was distributed within the cells.

Observations

(1) *Normal Blood*

Table I shows the data obtained from observations on a sample of normal blood. The horizontal array represents areas, arranged in class intervals of 2 mm. deflection, as shown by the galvanometer. The vertical array indicates the relative transparency, the class interval being 0.029. In this instance the correlation coefficient is +0.4877, a figure which is highly significant.

TABLE I
CORRELATION OF *area* AND *transparency*: 400 NORMAL HUMAN RED BLOOD CELLS,
STAINED WITH ACID FUCHSINE.

		AREA												
		3.	8.	36.	65.	96.	90.	53.	31.	10.	4.	3.	1.	400
TRANSPARENCY	0.301-.330 (incl.)			1.	1.									
	.331-.360													
	.361-.390	1.	3.	1.	1.					1.				
	.391-.420	2.		3.	3.	3.	3.	1.						
	.421-.450			5.	12.	7.	2.							
	.451-.480			3.	5.	8.	8.	8.	4.					
	.481-.510	1.	2.	6.	10.	17.	10.	4.	4.					
	.511-.540		2.	4.	13.	29.	21.	12.	3.	2.				
	.541-.570			4.	8.	14.	21.	15.	6.	3.				
	.571-.600			4.	5.	13.	16.	11 ⁶	12.	3.	1.			
TRANSPARENCY	.601-.630			1.	3.	3.	6.	5.	4.	2.	2.	3.		
	.631-.660				1.	1.	3.	1.	1.					1.
	.661-.690													
	.691-.720											1.		
		27. (incl.)	30. (incl.)	33. (incl.)	36. (incl.)	39. (incl.)	42. (incl.)	45. (incl.)	48. (incl.)	51. (incl.)	54. (incl.)	57. (incl.)	60. (incl.)	2.

The strictly linear nature of the regression line A/T is shown by Fig. 2. In plain terms these analyses indicate that, on a slide of normal blood, as ordinarily seen through the microscope, the larger cells appear paler than the smaller ones in definite proportion to their increased size.

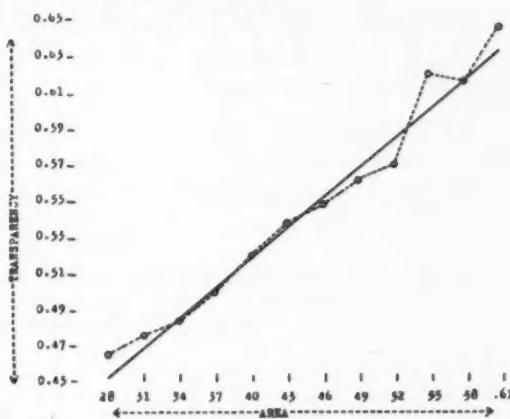
The frequency distribution curves of both area and transparency are essentially normal.

Similar data, obtained from other observations, have confirmed the belief that the example given is typical of normal blood.

(2) *Abnormal Blood*

Primary anemia. Table II gives the data obtained from a slide of blood, considered to have been typical of this condition. The following particulars relate to the case: No. D. 3; haemoglobin 76%; red cel-

FIG. 2. Means of transparency arrays and the regression line of transparency on area: computed from the data of Table I.



3.65 millions per cu. mm.; color index 1.04.

TABLE II

CORRELATION OF AGE AND transparency: 400 RED BLOOD CELLS FROM A CASE OF PRIMARY ANEMIA. STAINED WITH ACID FUCHSINE. AREAS INDICATED AS READ IN MM. OF GALVANOMETER SWING.

TRANSPARENCY AREA										AREA						
										66-71.	72-77	78-83	84-89	90-95	96-101	102-107
0.654-.670 (incl.)							1.	1.	1.							4.
.671-.687							2.	4.	0.	3.	2.					11.
.688-.704								3.	2.	1.	7.	3.	1.			17.
.705-.721								4.	3.	4.	4.	9.	4.	1.		29.
.722-.738	1.	1.	0.	3.	1.	4.	5.	6.	12.	9.	1.					43.
.739-.755					1.	1.	5.	8.	9.	16.	14.	2.				56.
.756-.772			3.	4.	2.	1.	10.	18.	12.	8.						58.
.773-.789					3.	1.	12.	12.	9.	22.	3.	0.	1.			63.
.790-.806		1.	0.	1.	1.	7.	19.	15.	12.	4.	0.	1.				61.
.807-.823						1.	0.	4.	7.	9.	4.					25.
.824-.840					1.	0.	0.	1.	5.	7.	6.					20.
.841-.857			1.	1.	2.	1.	0.	3.	1.							9.
.858-.874						1.	0.	3.								4.
		1.	3.	5.	16.	13.	48.	76.	83.	103.	45.	5.	2.	400		

In this instance, the correlation of area and transparency is -0.1563 . The figure is of more significance because of the negative sign preceding it than because of its size. It indicates that, per unit of area, the larger cells actually stained more deeply than the smaller ones.

The regression line, A/T , is non-linear and suggests heterogeneity.

The frequency distribution curve of the cell areas is negatively skewed and has a high mean value.

Secondary anemia. Case No. D.8; haemoglobin 43%; red blood cells 3.58 millions per cu. mm.; color index 0.61. A correlation surface, dealing with 393 cells from this patient, is shown as Table III.

TABLE III

CORRELATION OF AREA AND TRANSPARENCY OF 393 RED BLOOD CELLS FROM A CASE OF SECONDARY ANEMIA. STAINED WITH ACID FUCHSINE. AREAS INDICATED AS READ IN MM. OF GALVANOMETER DEFLECTION.

TRANSPARENCY	AREA												7. 13. 35. 50. 48. 69. 83. 37. 30. 15. 4. 2.		
	.91- .95	.95- .99	.95- .99	.99- .96	.99- .93	.99- .97	.94- .90	.98- .97	.98- .94	.95- .91	.95- .90	.101- .08	.101- .15	.101- .12	.101- .19
0.730- .746 (incl.)							1.	1.	0.	1.	2.	1.	1.		7.
.747- .763									2.	7.	2.	2.			13.
.764- .780						4.	1.	5.	5.	12.	6.	2.			35.
.781- .797			1.	0.	2.	9.	6.	11.	6.	10.	3.	2.			50.
.798- .814					1.	6.	8.	12.	6.	9.	1.	5.			48.
.815- .831	2.	0.	2.	1.	13.	17.	17.	7.	6.	3.	1.				69.
.832- .848		1.	1.	4.	13.	33.	19.	6.	4.	0.	1.	1.			83.
.849- .865					1.	6.	7.	18.	3.	1.	0.	1.			37.
.866- .882	1.	0.	0.	1.	9.	6.	9.	3.	1.						30.
.883- .899					5.	8.	1.	0.	0.	0.	0.	0.			15.
.900- .916					2.	0.	1.	0.	1.						4.
.917- .933								1.	1.						2.
	3.	1.	4.	8.	61.	90.	91.	50.	44.	23.	14.	3.	1.		393.

In this instance, the correlation of area and transparency is -0.3821 . The regression line is non-linear. The frequency distribution curve of cell areas is slightly but *positively* skewed and its mean value is high.

Case No. G.1; haemoglobin 15%; red blood cells 1.62 millions per cu. mm.; color index 0.46; anisocytosis very marked. The correlation surface for area and transparency of the stained cells is given as Table IV.

The correlation is $+0.4672$. Regression line A/T is non-linear. The frequency distribution curve of cell areas is *negatively* skewed and has an approximately normal mean value.

TABLE IV

CORRELATION OF *area* AND *transparency* OF 400 RED BLOOD CELLS FROM A CASE OF
SECONDARY ANEMIA, STAINED WITH ACID FUCHSINE. ARRAYS
AS IN PRECEDING TABLES.

TRANSPARENCY (incl.)	AREA												95-100
	23-28	29-34	35-40	41-46	47-52	53-58	59-64	65-70	71-76	77-82	83-88	89-94	
0.176-.222 (incl.)	1.	0.	0.	1.									2.
.223-.269		2.											2.
.270-.316		1.	0.	0.	0.	2.							3.
.317-.363			1.	0.	0.	1.							2.
.364-.410			2.	4.	2.	1.	1.	3.	4.				17.
.411-.457	1.	1.	3.	8.	3.	4.	4.	1.	1.	1.			27.
.458-.504	2.	2.	2.	6.	2.	6.	11.	7.	13.	3.			54.
.505-.551			2.	6.	11.	6.	9.	12.	15.	6.	5.	4.	1.
.552-.598				1.	5.	4.	9.	7.	13.	17.	20.	14.	7.
.599-.645					1.	4.	3.	6.	1.	5.	8.	12.	13.
.646-.692						1.	0.	2.	3.	0.	1.	7.	5.
.693-.739							1.	0.	0.	0.	2.	0.	3.
.740-.786								1.					1.
	4.	12.	26.	37.	29.	34.	48.	55.	59.	44.	32.	13.	6.
													1
													400.

Errors

The greatest source of error was concerned with making the silhouettes. It was a personal one and therefore inconstant. An attempt to assess it was undertaken by making 25 silhouettes of each of a number of blood cells, having different sizes and shapes, and by determining the uniformity of the results. In this way, it was found that, while large, round cells could be reproduced most accurately, small, irregularly shaped ones were troublesome unless great care and patience were exercised. Incidentally, the errors of area affected the figures representing staining intensity. Finally, there were minor inaccuracies, owing to the fact that every apparently blank field between the cells on the blood films did not transmit exactly the same amount of light. Consideration of these factors convinced the writers that the average probable error of their observations amounted to slightly less than $\pm 4\%$.

Discussion

(1) Areas and Area Variations

So far as normal blood is concerned, there is comparatively little to be said under this heading. The example given in Table I shows that the extreme figures representing areas are in about the same relative proportion as the squares of the diameters of the extremes for normal blood cells, given by Savage and Isa (6), *i.e.*, $(6)^2 : (9)^2 : 27 : 62$ (approx.). It was a matter of chance that the mean value of the areas, stated in mm. of galvanometer deflection, should have corresponded as closely as it did to the mean area

(of one side) of normal red blood cells in microns (40-42). The chance, however, was a very happy one, because it indicates that *all the figures for area roughly represent square microns*. But these remarks merely show that, compared to an established method, the use of silhouettes and photometer gave reliable results. It is evident that, when only the areas of circular cells are under consideration, the labor involved makes this technique impractical.

In dealing with other than circular cells, however, the method is applicable and diameter measurements fail. Ovoid, sickle-, star- and pear-shaped outlines are matters of indifference to a photometer. For this reason, it is contended that, in the case of grossly distorted cells, full information concerning their areas could be determined by this method.

It may be assumed that curves thus obtained show in *kind* all the variations of the well known Price-Jones (4) curves and do so to a greater degree. This phase of the subject has not been explored more thoroughly for the simple reason that, to the writers, area measurement was not an end in itself: rather it was a necessary step to the determination of staining intensity.

(2) *Staining Intensity and Its Variations*

One objectionable feature of the method was that the degree of saturation to which staining could be continued was fixed by the thickness of the plasma on the slides, and not by the corpuscles. To a slight extent, this must have interfered with the fair comparison of one cell with another on the same slide. As a matter of opinion, it rendered direct comparisons of the staining intensities of cells on different slides highly undesirable. For this reason, measurements of staining intensity in absolute terms were not attempted. But there is nothing to vitiate a comparison of the *trends* of staining in relation to the sizes of the cells, or, to continue with the expression already in use, of the A/T correlations of different specimens of blood.

Normal blood. In the case of normal blood, it has been observed that the regression of transparency on area is linear, and it is fitting that this should be considered in relation to the general law governing light absorption. The rate of the absorption of light passing through the stained blood cells depends on (i) the light source, (ii) the thickness of the cells and (iii) their staining intensity. The first of these being constant, only the two others need be considered.

If either of these factors were constant, the curve resulting from proportional changes in the other would be logarithmic. But the two curves would be in opposite directions. Hence, it seems reasonable to assume that the observed linear relation between area and transparency of a series of stained, normal blood cells is due to a compromise between the effects of thickness and staining intensity. In this compromise the latter effect predominates.

Pathological blood. It may be worth noting that, in relation to the cells of average size, deeper staining of the small cells and/or lighter coloring of the large ones have the same effect on the A/T correlation. They render it positive. Conversely, lighter colored small cells and/or more darkly stained large ones tend to make the correlation negative. There can be little doubt

that the numerical expression of this correlation varies within limits which have not been determined yet in the case of normal blood. For this reason and because of the small number of observations, it is impossible to enter into an extensive discussion of the ways in which the areas and staining intensities of blood cell populations depart from their normal limits during the course of any particular disease, with the possible exception of pernicious anemia. One can merely indicate departures which might take place, leaving it to workers with clinical facilities to determine the facts.

In retrospect, it is not remarkable that the blood cells from a case of typical pernicious anemia should have exhibited a negative A/T correlation. While that condition may not have been previously expressed in mathematical terms, hematologists have long assumed that it existed. The writers have merely demonstrated it by physical means. Incidentally, a negative A/T correlation is not of pathognomonic significance. Both positive and negative correlations have been found in cases of "secondary" anemia.

No other general statement is warranted concerning the "secondary" anemias examined. Unfortunately, an example of the microcytic type was not included.

All the pathological bloods exhibited non-linear A/T regression lines.

Summary

It has been shown that the areas of blood cells may be measured almost regardless of the forms in which they occur and that, statistically, the frequency distribution curves of these areas are highly instructive. This is complete extension of the work of Price-Jones (4) and Pijper (5).

The degrees of transparency of the stained individual cells may be obtained also. The transparencies (and staining intensities) of the cells of a series are related to the areas of the same cells either positively or negatively. Theoretically, there seems to be no reason why they might not be quite unrelated under certain pathological conditions.

Without wishing to add to the many systems of classification which have been proposed for pathological blood, the writers suggest that clarification of the subject might result if consideration were given to the area-transparency correlation which they have described.

Acknowledgments

Thanks are expressed to the physicians who furnished slides of pathological blood, particularly to Dr. L. S. P. Davidson of Aberdeen, Dr. O. Klotz of Toronto, Dr. J. D. Adamson and Dr. Alex Gibson of Winnipeg.

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THE ELECTRODYNAMIC CHARACTERISTICS OF THE QUARTZ PIEZOELECTRIC OSCILLATOR¹

BY JAMES W. SPEIGHT²

Abstract

The electro-acoustic properties of a piezoelectric oscillator in the form of a quartz-steel sandwich have been studied. The oscillator is assumed to be perfectly efficient and to be emitting divergent waves into the medium in which it is immersed. The arrangement of quartz to steel is investigated with a view to obtaining the best operating conditions of the oscillator. When the radius of the oscillator is infinite, the results reduce to those obtained when plane waves are emitted into the outside medium.

Section 1. Introduction

The general principles of construction of piezoelectric oscillators are briefly described in various textbooks on sound (9). The oscillator considered in the present paper consists of a disc of quartz placed between two steel plates of equal thickness, the outer surfaces of which are in contact with the same medium, so that radiation occurs equally on the two sides of the plane of symmetry.

The object of this paper is to discuss the electro-acoustic properties of such an oscillator. It is evident that the radiation field on either side of the plane of symmetry is equivalent to that generated by a piston surrounded by an infinite, rigid flange. In a number of recent papers by Biquard (1), amplifying lectures given by Langevin at the "Collège de France" (1923), the electro-acoustic properties of quartz-steel "sandwiches" are discussed at length. These calculations, however, refer to infinite radiating surfaces giving rise to plane waves in the medium. Although the characteristics so described may be applied to an actual transmitter of circumference very large compared with the wave-length, it is of some interest to determine the electro-acoustic characteristics of a transmitter of finite radius.

An exact treatment of the properties of the radiation field have been worked out by King (4), so that it is now possible to determine theoretically the acoustic output of a transmitter as described above. For a given radius and frequency, this will obviously depend on the thickness of quartz and steel plates, resonance in the latter being largely responsible for a high output, and the aim of this paper is to determine as closely as possible the optimum output and resonance characteristics. This is all the more important inasmuch as King (4) has shown that, owing to the viscosity of water, there is an optimum range of transmission, depending on the radius of the transmitter, requiring frequencies which make the ratio of circumference to wave-length comparatively small (about 5 or 6). In these circumstances, there is also an optimum radius for the transmitter, the determination of which is of

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considerable interest to the designer. In order to simplify the problem, adial modes of vibration in the quartz-steel sandwich are not considered, although a reference to Section 8 of King's paper shows that there is a rapid fluctuation of pressure over a radiating piston which would undoubtedly set up radial, flexural and compressive waves in the steel disc. The mathematical consideration of these waves is likely to be extremely difficult and is beyond the scope of the present paper. We therefore imagine the surface of the steel plate in contact with water to be covered by a thin, perfectly rigid disc of equal radius, so that the elastic waves in quartz and steel are in one dimension only. Also the dissipation of energy in quartz and steel is neglected, although the inclusion of this factor could, if necessary, be taken into account.

Section 2. Theory

The conditions of the problem are:—

1. The central plane of the quartz disc undergoes no displacement and is selected as the plane of reference $z=0$.
2. The pressures at the surfaces of separation are equal and continuous.
3. The displacements at the surfaces of separation are continuous.

The arrangement of the oscillator is shown in Fig. 1. The radial oscillations are not considered in the steel and quartz, and the energy dissipation is assumed negligible. The wave motion is of the type (2, 7)

$$\frac{\partial^2 r}{\partial z^2} = \rho \alpha \frac{\partial^2 r}{\partial t^2} = \frac{1}{c^2} \frac{\partial^2 r}{\partial t^2},$$

where c is the velocity of propagation, ρ is the density of the medium and α is the coefficient of compressibility.

In the problem dealt with here, the displacement velocity $\dot{r} = |\dot{r}| e^{i\omega t}$ is desired. The general solution is

$$\dot{r} = A_1 \cos \kappa z + A_2 \sin \kappa z,$$

in which $\kappa = \omega/c = 2\pi/\lambda$.

In order to satisfy condition 1, the solution must be

$$\dot{r} = A_2 \sin \kappa z.$$

If \dot{r}_q is the velocity at any time at $z=l$, and $\epsilon = \kappa l$,

$$A_2 = \dot{r}_q \operatorname{cosec} \epsilon.$$

The appropriate solution for the quartz is

$$\dot{r} = \dot{r}_q \operatorname{cosec} \epsilon \sin \kappa z. \quad (1)$$

Let the quantities referring to steel be denoted by the subscript 1. Then the solution for the steel has the form

$$\dot{r}_1 = B_1 \sin \kappa_1 (z-l) + B_2 \sin \kappa_1 (z-l-\epsilon).$$

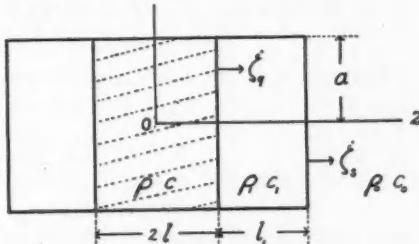


FIG. 1. Schematic diagram of the oscillator.

If $\dot{\xi}_s$ is the velocity at the surface of the steel at any time, condition 3 requires that

$$\dot{\xi}_1 = \dot{\xi}_s \text{ at } z = l ;$$

$$\dot{\xi}_1 = \dot{\xi}_s \text{ at } z = l + l_1 .$$

The coefficients are given by

$$B_1 = \dot{\xi}_s \operatorname{cosec} \epsilon_1 ,$$

$$B_2 = - \dot{\xi}_s \operatorname{cosec} \epsilon_1 , \text{ where } \epsilon_1 = \kappa_1 l_1 .$$

Hence, the solution for the steel is

$$\dot{\xi}_1 = \dot{\xi}_s \operatorname{cosec} \epsilon_1 \sin \kappa_1(z-l) - \dot{\xi}_s \operatorname{cosec} \epsilon_1 \sin \kappa_1(z-l-l_1) . \quad (2)$$

After differentiation with respect to the time, the continuity of pressures at $z = l$ gives

$$- \frac{1}{\alpha} \frac{\partial \dot{\xi}_1}{\partial z} + i\omega \bar{\omega}_1 = - \frac{1}{\alpha_1} \frac{\partial \dot{\xi}_1}{\partial z} ,$$

since

$$\bar{\omega}_1 = |\bar{\omega}_1| e^{i\omega t} .$$

That is,

$$- \dot{\xi}_s \frac{\kappa}{\alpha} \cot \epsilon + i\omega \bar{\omega}_1 = - \frac{\kappa_1}{\alpha_1} (\dot{\xi}_s \operatorname{cosec} \epsilon_1 - \dot{\xi}_s \cot \epsilon_1) .$$

If we put $m = \kappa \alpha_1 / \kappa_1 \alpha$ and $A_o = \omega \bar{\omega}_1 \alpha_1 / \kappa_1$ and rearrange,

$$- \dot{\xi}_s \operatorname{cosec} \epsilon_1 + \dot{\xi}_s (\cot \epsilon_1 + m \cot \epsilon) = i\omega A_o . \quad (3)$$

The factor $\bar{\omega}_1$ is the internal piezoelectric pressure given by (1, p. 115, Equation 27)

$$\bar{\omega}_1 = \frac{Q\delta}{2C\alpha_o} ,$$

where Q is the total charge on surface of the crystal,

δ is the piezoelectric constant,

C is the capacity at constant thickness,

and α_o is the compressibility at constant field.

Now, at the surface of the steel plate and the medium the longitudinal wave motion is replaced by a divergent wave represented by the velocity potential (4)

$$\phi = a_2^* \int_0^\infty e^{-\mu(z-l-l_1)} J_0(\lambda r) J_1(\lambda a) \frac{d\lambda}{\mu} ; \quad \mu = (\lambda^2 - \kappa_0^2)^{\frac{1}{2}} .$$

The total pressure on the diaphragm is

$$\begin{aligned} P_o &= \int_0^a \rho_o (\phi)_{z=l+l_1} 2\pi r \cdot dr \\ &= 2\pi \rho_o a^2 \dot{\xi}_s \int_0^\infty J_1^2(\lambda a) \frac{d\lambda}{\mu \lambda} \\ &= 2\pi \rho_o a^2 \dot{\xi}_s M , \end{aligned}$$

where M is a complex number with real component $M_1 = H_1(2\kappa a) / 2\kappa^2 a$ and imaginary component $M_2 = (1 - J_1(2\kappa a) / \kappa a) / 2\kappa$.

After differentiation with respect to the time, the continuity of pressures at $z = l + l_1$ gives

$$- \frac{\pi a^2}{\alpha_1} \frac{\partial \dot{\xi}_1}{\partial z} = \dot{P}_o . \quad (4)$$

But, since $\dot{\zeta}_s = |\dot{\zeta}_s| e^{i(\omega t-\phi)}$, $\ddot{\zeta}_s = -\omega^2 \dot{\zeta}_s$. Relation (4) becomes
 $\kappa_1(\dot{\zeta}_s \cot \epsilon_1 - \dot{\zeta}_s \operatorname{cosec} \epsilon_1) = 2\rho_o \alpha_1 c_1 \omega^2 M \dot{\zeta}_s$.

If we put $\beta = 2\rho_o \alpha_1 c_1 \omega$ in the above,

$$\dot{\zeta}_s(\cot \epsilon_1 - \beta M) - \dot{\zeta}_s \operatorname{cosec} \epsilon_1 = 0. \quad (5)$$

Equations (3) and (5) give

$$\dot{\zeta}_s = \frac{i\omega A_o \operatorname{cosec} \epsilon_1}{(\cot \epsilon_1 - \beta M)(\cot \epsilon_1 + m \cot \epsilon) - \operatorname{cosec}^2 \epsilon_1}.$$

By using the substitutions

$$N_1 = \sin \epsilon \cos \epsilon_1 + m \cos \epsilon \sin \epsilon_1$$

and

$$N_2 = \sin \epsilon \sin \epsilon_1 - m \cos \epsilon \cos \epsilon_1,$$

the velocity of the diaphragm is

$$\dot{\zeta}_s = \omega A_o \sin \epsilon / \Delta, \quad (6)$$

where $\Delta = \beta M_2 N_1 + i(N_2 + \beta M_1 N_1)$, with argument θ .

Similarly, the deformation of half the quartz crystal is

$$\dot{\zeta}_q = \omega A_o \Delta_1 \sin \epsilon / \Delta, \quad (7)$$

where $\Delta_1 = \cos \epsilon_1 - \beta(M_1 - iM_2) \sin \epsilon_1$, with argument θ_1 .

Section 3. Acoustic Energy-resonance

It is evident from Equation (6) that

$$\dot{\zeta}_s = |\dot{\zeta}_s| e^{i(\omega t-\theta)},$$

where

$$|\dot{\zeta}_s| = \omega |A_o| \sin \epsilon / |\Delta|.$$

The acoustic power is

$$\frac{dW}{dt} = P_o \dot{\zeta}_s = 2\pi \rho_o a^2 \dot{\zeta}_s \dot{\zeta}_s M.$$

When P_o and $\dot{\zeta}_s$ are expressed as real quantities,

$$\frac{dW}{dt} = 2\pi \rho_o a^2 \omega |\dot{\zeta}_s|^2 [-M_1 \sin(\omega t - \theta) + M_2 \cos(\omega t - \theta)] \cos(\omega t - \theta).$$

The time average value is

$$\overline{\frac{dW}{dt}} = \pi \rho_o a^2 \omega M_2 |\dot{\zeta}_s|^2. \quad (8)$$

The maximum acoustic power depends on $|\dot{\zeta}_s|^2$ when the frequency and radius are fixed. If the thickness of the quartz is given, the quantity $|\dot{\zeta}_s|^2$ is a maximum when $|\Delta|^2$ is a minimum with respect to ϵ_1 . From Equation (6)
 $|\Delta|^2 = F(\epsilon_1) = \beta^2 N_1^2 (M_1^2 + M_2^2) + N_1^2 + 2\beta M_1 N_1 N_2$.

The condition for a minimum requires that

$$\begin{aligned} \frac{dF}{d\epsilon_1} &= \beta^2 (M_1^2 + M_2^2) 2N_1 \frac{dN_1}{d\epsilon_1} + 2N_2 \frac{dN_2}{d\epsilon_1} + 2\beta M_1 (N_1 \frac{dN_2}{d\epsilon_1} + N_2 \frac{dN_1}{d\epsilon_1}) \\ &= 2[N_1 N_2 (1 - \beta^2 (M_1^2 + M_2^2)) + \beta M_1 (N_1^2 - N_2^2)] \\ &= 0. \end{aligned}$$

The value of β is small; e.g., $\rho_o = 1.0$ gm./cc., $c_1 = 4.5 \times 10^5$ cm./sec., $\alpha_1 = 6.25 \times 10^{-13}$ cm.²/dyne, $\omega = 2.5 \times 10^5$ rad./sec., so that

$$\beta = 2\rho_o \alpha_1 c_1 \omega = 0.140 \text{ cm.}^{-1}.$$

The values of M_1 and M_2 are found by the use of graphs (5, p. 54, Fig. 17). For $\kappa \geq 1$,

$$k = \frac{1 - \beta^2(M_1^2 + M_2^2)}{\beta M_1}$$

is a positive quantity. In problems of practical interest, $\kappa > 1$ and there is no advantage in discussing the lower limit which κ may approach.

The condition for resonance becomes

$$N_1^2 + kN_1N_2 - N_2^2 = 0. \quad (9)$$

The equation has two roots, *viz.*,

$$N_1 = \frac{1}{2}N_2\{-k \pm (k^2 + 4)^{\frac{1}{2}}\}. \quad (10)$$

The second derivative of $F(\epsilon_1)$ is,

$$\frac{d^2F}{d\epsilon_1^2} = 2\beta M_1[k(N_1^2 - N_2^2) - 4N_1N_2].$$

For

$$N_1 = \frac{1}{2}N_2\{-k - (k^2 + 4)^{\frac{1}{2}}\},$$

$$\frac{d^2F}{d\epsilon_1^2} = \beta M_1 N_2^2 (k^2 + 4) \{k + (k^2 + 4)^{\frac{1}{2}}\} = \text{a positive quantity.}$$

Thus, the relation for maximum rate of radiation of energy is

$$N_1 = \frac{1}{2}N_2\{-k - (k^2 + 4)^{\frac{1}{2}}\} \\ = -bN_2.$$

Therefore

$$\tan \epsilon_1 = (mb - \tan \epsilon)/(m + b \tan \epsilon). \quad (11)$$

For large values of a ($ka = 2\pi a/\lambda \gg 1$),

$$H_1(2\pi a) \sim 2/\pi; \quad 1 - J_1(2\pi a)/ka \sim 1.$$

Hence

$$M_1 \sim 1/\pi a^2; \quad M_2 \sim 1/2\kappa.$$

If a becomes infinite, M_1 approaches zero. The quantity k becomes very large and

$$b \sim k \rightarrow \infty.$$

In this case

$$\tan \epsilon_1 = m \cot \epsilon. \quad (12)$$

Relation (12) is in agreement with the work of Biquard for plane waves in the outside medium. The concept of a disc of infinite radius is equivalent to the emission of plane instead of divergent waves into the medium. The energy function transforms into a function of ϵ which was taken at an arbitrary fixed value. There is then a value of ϵ which will produce the optimum maximum acoustic power.

At resonance, it is easily shown that

$$N_1 = \frac{b \cos \epsilon_1 (\sin^2 \epsilon + m^2 \cos^2 \epsilon)}{m \cos \epsilon + b \sin \epsilon},$$

$$N_2 = \frac{-\cos \epsilon_1 (\sin^2 \epsilon + m^2 \cos^2 \epsilon)}{m \cos \epsilon + b \sin \epsilon}.$$

Thence

$$|\Delta|^2 = \frac{\cos^2 \epsilon_1 (\sin^2 \epsilon + m^2 \cos^2 \epsilon)^2}{(m \cos \epsilon + b \sin \epsilon)^2} [\beta^2 M_1^2 b^2 + (\beta M_1 b - 1)^2].$$

Also,

$$\begin{aligned}\cos^2 \epsilon_1 &= 1/(1 + \tan^2 \epsilon_1) \\ &= \frac{(m \cos \epsilon + b \sin \epsilon)^2}{(1 + b^2)(\sin^2 \epsilon + m^2 \cos^2 \epsilon)}.\end{aligned}$$

At resonance, the acoustic power from each surface is

$$\left. \frac{d\bar{W}}{dt} \right|_R = \frac{\pi \rho a^3 \omega^3 |A_o|^2 M_1 (1+b^2)}{[\beta^2 M_1^2 b^2 + (\beta M_1 b - 1)^2] (1 + m^2 \cot^2 \epsilon)} . \quad (13)$$

Of course, there are two radiating surfaces and the total acoustic output is twice Expression (13).

Numerical Example

$\rho = 2.5 \text{ gm./cc.}$, $\alpha = 2.7 \times 10^{-12} \text{ cm.}^2/\text{dyne}$; $\rho_1 = 7.8 \text{ gm./cc.}$, $\alpha_1 = 6.25 \times 10^{-13} \text{ cm.}^2/\text{dyne}$. For a disc of radius 30 cm. and radiation of wave-length 3.77 cm., $\kappa = 1.67$. $M_1 = 3.8 \times 10^{-3}$; $M_2 = 0.30$. Hence $b \sim k = 1880$, $m = \rho c / \rho_1 c_1 = 0.356$. The general condition of resonance, for $\epsilon = \pi/4$, is

$$\begin{aligned}\tan \epsilon_1 &= (mb - 1)/(m + b) \\ &= 0.355 ,\end{aligned}$$

agreeing with Condition (12),

$$\tan \epsilon_1 = m = 0.356 .$$

Section 4. Electrical Power

The electromotive force across a piezoelectric crystal is given (1, p. 113) by $V = Q/C - 4\pi \delta \xi_q / K_1 \alpha_o$, in which the units are electrostatic.

Since $V = V_o e^{i\omega t}$,

$$I = \dot{Q} = i\omega CV + 4\pi C \delta \xi_q / K_1 \alpha_o . \quad (14)$$

The first term is a capacitance effect only. The current due to the capacity is additive, so that the equivalent electrical circuit (8) is a parallel circuit with one branch containing a condenser and the other an impedance. The power factor is zero for a perfect condenser and the electrical power can be associated entirely with the impedance arm.

The total velocity of the quartz surfaces is twice ξ_q . Hence the current in the impedance arm is

$$I = \frac{\pi a^2 \delta \omega |A_o| |\Delta_1| \sin \epsilon}{|\Delta| \alpha_o} e^{i(\omega t + \theta_1 - \theta)} .$$

The time average value of the product of the real parts of I and V gives the electrical power

$$P = \frac{\pi a^2 \delta \omega |A_o| |\Delta_1| V_o \sin \epsilon}{2 |\Delta| \alpha_o} \cos (\theta_1 - \theta) . \quad (15)$$

But

$$\begin{aligned}|A_o| &= \delta Q_o / 2 C \alpha_o \omega \rho_1 c_1 \\ &= \delta \beta V_o / 4 \pi \omega^2 \rho_o \alpha_o , \quad \text{using} \quad Q_o = CV_o .\end{aligned}$$

The electrical power becomes

$$P = \frac{2 \pi a^2 \omega^2 \rho_o |A_o|^2 |\Delta_1| \sin \epsilon}{\beta |\Delta|} \cos (\theta_1 - \theta) .$$

Now,

$$\begin{aligned}\cos(\theta_1 - \theta) &= \cos \theta_1 \cos \theta + \sin \theta_1 \sin \theta, \\ &= \beta M_1 (N_1 \cos \epsilon_1 + N_2 \sin \epsilon_1) / |\Delta| |\Delta_1| \\ &= \beta M_1 \sin \epsilon / |\Delta| |\Delta_1|.\end{aligned}$$

The power input is

$$P = \frac{2\rho_0 \pi a^3 \omega^3 M_1 |A_0|^2 \sin^2 \epsilon}{|\Delta|^2}. \quad (16)$$

The electrical input is equal to the acoustic output. The oscillator is 100% efficient. This agrees with the hypothesis that no energy is dissipated in the quartz or steel. The actual loss of energy in the quartz is due to two factors, acoustic and electrical dissipation. The dielectric losses in crystals are treated by Joffé (3).

Section 5. Optimum Maximum Power

The condition of optimum maximum power is found by examining the acoustic output at resonance. From the previous section, it is seen that $|A_0|$ is proportional to $1/l$, or, more conveniently $1/\epsilon$. The acoustic power is now proportional (Equation (13)) to

$$1/\epsilon^2(1 + m^2 \cot^2 \epsilon). \quad (17)$$

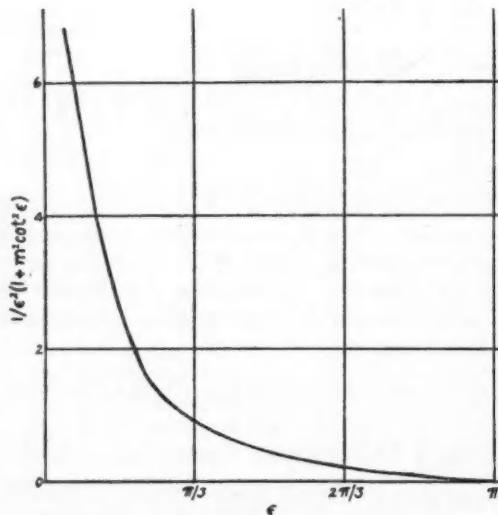


FIG. 2. Graph showing the rate of acoustic radiation at resonance.

The function is shown graphically in Fig. 2. There are no maxima in the range 0 to π , but the function approaches infinity for very small values of ϵ .

For $2l \ll \lambda$, ϵ is very small. Function (17) reduces to $1/\epsilon^2(1 + m^2/\epsilon^2) \sim 1/m^2$.

However, there is a practical limit to the thickness of the quartz, as it is necessary to select a point on the curve for which the quartz will not break down under the applied voltage. It is also very doubtful whether the quartz crystal will oscillate when the thickness is very small.

There is a critical voltage for a given thickness of quartz, above which the quartz will be punctured. The assumption is made that the voltage amplitude is proportional to the thickness of the quartz, i.e., $V_0 \propto \epsilon$.* Since $|A_0|$ is proportional to V_0/ϵ , the output of acoustic energy is proportional

* The limitations and validity of the assumption may be found in References (3, 6).

to $1/(1+m^2 \cot^2 \epsilon)$. The maximum rate of acoustic radiation is obtained for $\cot \epsilon = 0$, or, $\epsilon = \pi/2$.

The thickness of quartz at this point is

$$2l = \pi c/\omega = 3.14 \times 5 \times 10^8 / 2.5 \times 10^6 \\ = 6.3 \text{ cm.}$$

For this case, the thickness of steel is zero as determined by the resonance condition.

Section 6. Summary

1. By the use of the velocity potential ϕ for divergent waves and the displacement velocity $\dot{\zeta}$ for plane waves, the velocities $\dot{\zeta}_q$ and $\dot{\zeta}_s$ at the surfaces of the quartz and steel respectively are obtained.

2. The acoustic power is determined in terms of physical quantities which are known. The theory is valid when the oscillator is immersed in any medium, although the calculations in this paper are those for water.

3. The condition of resonance between the thicknesses of the quartz and steel is found to be

$$\tan \epsilon_1 = (mb - \tan \epsilon) / (m + b \tan \epsilon) ,$$

which reduces to $\tan \epsilon_1 = m \cot \epsilon$ for a very large radius.

4. The optimum maximum power is produced theoretically when a very thin disc of quartz is used. If one assumes that there is a critical voltage proportional to the thickness of the quartz, the optimum maximum occurs when the quartz is 6.3 cm. thick.

Acknowledgment

The writer wishes to thank Dr. L. V. King who suggested and supervised the problem.

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STARCH CONTENT OF SOME SAMPLES OF CANADIAN WHEAT¹By CLARENCE YARDLEY HOPKINS² AND RONALD P. GRAHAM³**Abstract**

Average samples of seven grades of western Canadian wheat (1933 crop) were analyzed for starch by a polarimetric method. The mean starch content was 51.46%, on a basis of 13.5% moisture. The variation among the grades was small. Protein content varied inversely with starch, but the sum of the two decreased from the higher to the lower grades. The relation of starch content to flour yield is discussed.

Introduction

During a survey of possible industrial uses for Canadian wheat, it was observed that the most likely processes make use of the starch in the grain and that the remaining constituents become by-products. This would be the case in the manufacture of wheat starch, the production of alcohol, or the fermentation to acetone and *n*-butanol.

It was desirable, therefore, to know the starch content of Canadian wheat, not only for the purpose of comparing wheat with other carbohydrate raw materials, but also for the determination of the relative value of the various grades for industrial purposes.

A study of wheat by grades was carried out by Saunders and Shutt in 1908 (11), but the analyses did not include the determination of starch. The only figure for the starch content of Canadian wheat which the authors have been able to find is in a paper by Herd and Kent-Jones (7). They report 51.5% starch in a sample of No. 3 Northern.

There has been a lack of satisfactory methods for the estimation of starch, and this accounts in part for the fact that it is usually omitted from the ordinary analysis of agricultural products. Earlier in the investigation a convenient polarimetric method was perfected (8), and it was used throughout the present study.

The samples of grain were furnished in May 1934 by the Chief Inspector of Grain of the Board of Grain Commissioners at Winnipeg. They were average samples of each of seven grades for the 1933 crop. The sample of Marquis wheat grown in Ontario was supplied by the Cereal Division, Central Experimental Farm, Ottawa.

Experimental

The wheat was cleaned by hand and all weed seeds, foreign grains, straw and hulls were removed. Shriveled and immature wheat kernels were left in the samples.

The grain was ground in a Wiley mill and special precautions were taken to ensure that no material was blown out of the mill. The hopper and the screen were blocked out with paper, and the sample was ground and sifted

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alternately until about 75% passed through a 100 mesh sieve. The oversize was ground by hand in a mortar until only the bran (about 12% of the sample) failed to pass through the 100 mesh sieve. The bran was then mixed thoroughly with the fine material.

Moisture was determined by heating for five hours at 100° C. *in vacuo*. Check determinations were made after the starch analyses had been completed, and the moisture content was found to be virtually unchanged.

The results of the starch determinations are given in Table I.

TABLE I
STARCH CONTENT OF CANADIAN WHEAT

Grade of wheat	Moisture, %	Starch, % (as received)	Starch, % (13.5% moisture basis)
1 Northern	11.15	(53.16, 53.41)	Av. 51.88
2 Northern	11.06	(53.49, 53.44)	52.00
3 Northern	10.70	(51.79, 51.70)	50.13
4 Northern	10.73	(52.66, 52.66)	51.03
No. 5 wheat	10.52	(53.81, 53.75)	51.99
No. 6 wheat	10.56	(53.17, 53.22)	51.45
Feed wheat	10.37	(53.69, 53.49)	51.72
Ontario Marquis	10.84	(53.55, 53.82)	Av. 51.46 52.08

Weight per measured bushel was determined by weighing a sample of the grain in a graduate as suggested by Aamodt and Torrie (1). A 100 cc. graduate was used, but the agreement between duplicates was not as good as might be desired.

The specific gravity of the kernels was determined by the pycnometer method of Bailey and Thomas (4).

A graphical comparison of specific gravity, starch content and weight per measured bushel is shown in Fig. 1. Schmorl reports that the specific gravity

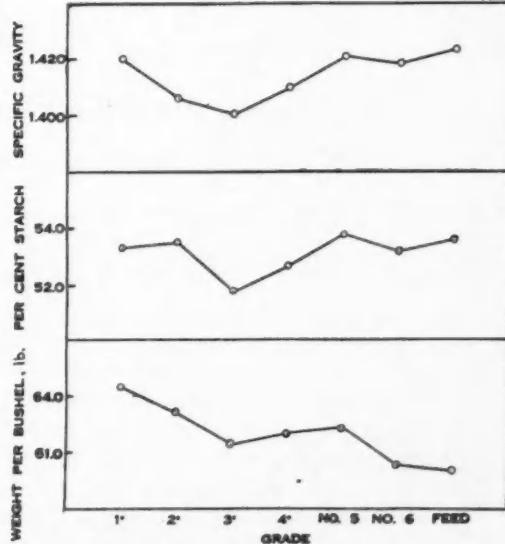


FIG. 1. Comparison of starch content of wheat with physical properties of the kernels. Moisture basis, as received.

of wheat varies directly with the starch content (12), and the present results appear to confirm this relation to some extent. However, as Bailey points out, comparisons of this sort should be restricted to wheats of the same type or variety (3).

Protein Content

Protein was determined by the official Kjeldahl method, and the results are plotted in Fig. 2.

There is evident a tendency for the content of starch to vary inversely with that of protein. Thus the sample of Grade 3, which has the lowest percentage of starch, is highest in protein.

The sum of the percentages of protein and starch, plotted in the lowest section of the graph, decreases to some extent from the higher to the lower grades. The differences are small, however, and this would lead to the conclusion that the feeding value of the lower grades of wheat is almost as high as that of the top grades.

During the starch analyses, the preliminary washing of the ground samples with aqueous alcohol was carried out in identical manner in each case, and the washings were made up to known volume and examined in the polarimeter. Though the optical rotation of the solution is due to several constituents, it is essentially a measure of the amount of dissolved protein. It was found that the amount of dissolved protein deter-

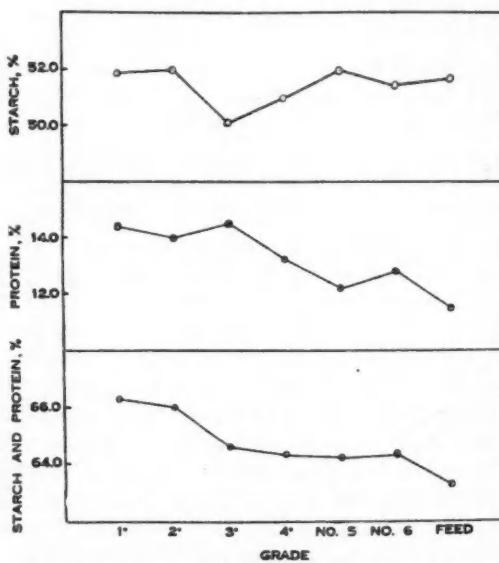


FIG. 2. Comparison of starch content with protein content of wheat. Moisture basis, 13.5%.

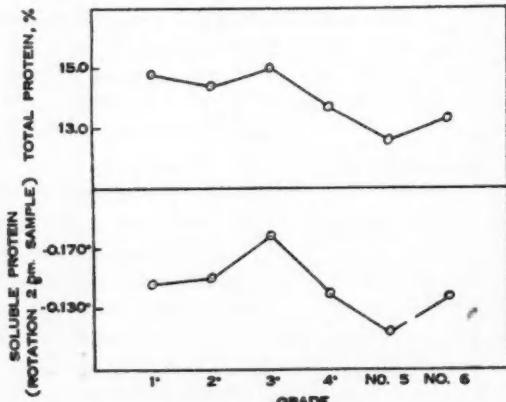


FIG. 3. Comparison of total protein with protein dissolved during washing with aqueous alcohol. Moisture basis, as received.

mined in this way varied from grade to grade in the same general way as the amount of total protein. The two are compared graphically in Fig. 3.

Discussion of Results

Comparison with other Analyses of Wheat

The results for starch content are somewhat lower than would be expected from statements in textbooks and elsewhere, which give the starch content of wheat as 60 to 70% (2, 5, 10). This error seems to arise from the fact that carbohydrates as a group are usually determined by difference, and this carbohydrate portion is regarded as consisting almost entirely of starch. In this way the hemicelluloses and related constituents are overlooked. Confusion also arises when the moisture content is not clearly stated.

Canadian hard wheat is relatively high in protein and hence its content of starch may be proportionately lower than that of soft European or southern wheats. This statement is borne out by the results of recent analyses which are shown in Table II.

TABLE II
STARCH CONTENT OF VARIOUS WHEATS
(13.5% moisture basis)

Source	Type	Starch, %	Method	Reference
Western Canada	Hard spring	51.5	Polarimetric	Present work
Western Canada	No. 3 Northern	51.5	Rask	7
United States	—	50.0-58.5	Diastase	9
Argentine	—	51.9	Rask	7
—	Durum	54.0	Rask	7
England	—	54.2	Rask	7
United States	—	56.7	Polarimetric	8
Ontario	Soft winter	59.1	Polarimetric	8

It will be noted that in none of these samples was the starch content as high as 60%.

Starch Content and Flour Yield

The small variation in starch content among the seven grades of Canadian hard wheat was quite unexpected. It was shown definitely by Geddes, Malloch and Larmour (6) that flour yield from wheat of the 1928 crop diminished from Grades 2 to 6, and it was thought that flour yield would be closely related to starch content. Judging from the present work, there is no direct relation. It must be concluded that flour yield depends more on the physical condition of the bran and the resultant ease of separation of bran from endosperm than on the actual amount of endosperm.

The inclusion of the so-called "starchy" kernels in the lower grades may have the effect of raising their average starch content.

It should be noted also that more variation from year to year is to be expected in the lower grades than in Grades 1 to 4, since the definitions of the latter are fixed by statute. The crop of 1933 was of high quality and the wheat in Grades 5, 6 and Feed was consequently of better than average quality.

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THE HYDROGENATION OF ALBERTA COALS

I. PRELIMINARY EXPERIMENTS ON SUSPENSION MEDIA AND CATALYSTS WITH THREE COALS¹

BY E. H. BOOMER² AND A. W. SADDINGTON³

Abstract

The action of five suspension media and various catalysts in the hydrogenation of coal has been investigated. It has been shown that the Alberta coals used may be hydrogenated successfully. The properties of the medium have been found to be a controlling factor in the process. The effectiveness of the different media varied with the ease with which they could be hydrogenated and dehydrogenated. Tetrahydronaphthalene was found to be much superior to other media, and showed a greater effect than could be attributed to any of the catalysts used. Experiments showed that this compound was effective because of its action as a hydrogen carrier. Of the catalysts used, molybdc oxide and a mixture of iron and chromium oxides were most effective. The details of the reactions are discussed briefly.

Introduction

The production of oil from coal by reduction with hydrogen at high pressures and temperatures has received considerable attention as offering now or in the future a source of motor and fuel oils. Moreover, the study of the reactions may result in an appreciable extension to the knowledge of the constitution and properties of coal. Reference may be made, for example, to the pioneer work of Berthelot (7), of Fischer and co-workers (11, 12), and to the essential development work of Bergius, Graham and Dunstan (5, 6, 10, 13) leading to commercial application of the process. More recently, a large body of work has been reported covering extensive experiments in Great Britain and Germany, with smaller contributions from numerous other nations (16, 22-26, 30), the literature of which is voluminous and best reviewed in the proceedings of various international coal and power conferences. The general principles of the process and the technique of their application to coal and other carbonaceous material are well known.

The present work is a continuation of investigations dealing with Alberta bitumens as applied to coal, and was undertaken because of the vast resources of low grade coals and the possibility of cheap hydrogen from coal or natural gas in Alberta (2, 3, 4, 18), together with the absence, at present, of adequate petroleum fields. Apart from brief references to the present work (in Reports of the Research Council of Alberta) there appear to have been only two other similar studies on North American coals, one by Beuschlein on United States coals (8) and one by Graham on Alberta coal (15). The necessity for studies on Alberta coals was made apparent by preliminary experiments some years

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ago with coal in a simple autoclave using a mechanical stirrer. These experiments showed the possibility of reduction of Alberta coals, and also showed the necessity of an investigation to determine the optimum conditions of operation, which could not be predicted from other work. The extension of the work beyond a routine test resulted from the belief that the procedure could be improved, and from the discovery that the nature of the suspension medium was as important as that of the catalyst and the coal.

These experiments deal primarily with the best suspension medium and the best catalyst for effecting the greatest conversion of coal to liquids, with the formation of the minimum amount of solid residue. The chemical and physical properties of the oils were considered to be of secondary importance. A second paper will present data of a comparative nature on a graded series of Alberta coals including all ranks. It has been found that with the same coal, whatever the rank, the effect of changing the suspension medium is more pronounced and of more practical interest than that of changing the catalyst, within the limits of the present work. Of the five media used, one, tetrahydronaphthalene, commonly termed tetralin, has been found to be much superior to all others, and produces an increased rate of reaction and yield beyond any effect produced by the catalysts employed. The practical value of tetralin as a medium may not appear great in view of its present cost. It can be largely recovered from the products, however, and moreover is essentially an inexpensive material when prepared in quantity from naphthalene. In addition, naphthalene and related compounds which are readily converted to tetralin and related compounds of nearly equivalent efficiency in the reaction, may be obtained at low cost in the future by pyrolysis of natural gas.

Materials and Apparatus

The three coal samples studied were among those taken in the 1929 Alberta Coal Survey and were made available through the kindness of Prof. E. Stansfield of the Research Council of Alberta. The origin, classification

and analysis of these coals as received are shown in Table I. The choice of coals, though somewhat arbitrary, was made on the basis of their probable susceptibility to destructive hydrogenation with the formation of oils. The coals were dried at 125° C. in an inert atmosphere of natural gas at a pressure of 20 mm. of mercury, and were then ground to pass a 100 mesh screen in

TABLE I
CLASSIFICATION AND ANALYSIS OF COAL SAMPLES;
ALBERTA COAL SURVEY 1929

Sample No.	419	420	424
Origin	McLeod River Colliery	Pincher Creek— 295	Drumheller— 678
Canadian classifica- tion	Sub-bitu- minous	Bitumi- nous	Lignite
Moisture, %	6.2	2.2	15.2
Ash, %	10.1	9.2	8.2
Volatile matter, %	38.3	32.5	31.4
Fixed carbon, %	45.4	56.1	45.2
Nitrogen, %	0.6	0.9	
Sulphur, %	0.5	0.8	

a ball mill containing an atmosphere of natural gas. They were stored in stoppered glass bottles.

Five different materials were employed as suspension media in making up coal pastes. The first was a residual oil of I.B.P. 225° C. from the distillation of hydrogenated McMurray bitumen. It was a mixed base oil containing paraffins, naphthenes, traces of olefines and about 15% of asphaltic material. It was highly unstable, cracked at 250 to 275° C., and deposited gums on standing. The second material was crude McMurray bitumen supplied by Dr. K. A. Clark of the Research Council of Alberta. This material was merely dried at 110° C. before use; it contained about 1% mineral matter. The third material was a medicinal paraffin oil of American origin sold under the name Liquid Petrolatum, Heavy, B.P. It was water white, saturated, I.B.P. 300° C.; 95% distilled over at 400° C. without decomposition at atmospheric pressure. The fourth material was phenol, U.S.P. grade, crystals. The last was tetrahydronaphthalene of Eastman practical grade, b.p. 202-204° C. This material will be referred to hereafter by its common name, tetralin.

The hydrogen used was the commercial electrolytic product as ordinarily supplied at 100 atm. in steel cylinders. Occasionally Viking natural gas as supplied locally was used, and also water gas prepared by partial oxidation of natural gas over a nickel catalyst. The Viking gas was 93% methane, the rest being mostly nitrogen with small amounts of ethane and propane. The composition of the water gas was approximately as follows:- Hydrogen, 65.7; carbon monoxide, 32.8; nitrogen, 1.5%. All gases were free from sulphur compounds and, after passage over solid potassium hydroxide, were stored under pressure in steel cylinders connected through appropriate control valves to the autoclave.

Five different catalysts have been used. They were ammonium molybdate, molybdc oxide, chromic oxide, an equimolar mixture of chromic and molybdc oxides, and an equimolar mixture of chromic and ferric oxides. Molybdc oxide was prepared by decomposition of ammonium molybdate at red heat. Chromic oxide and ferric oxide were prepared by precipitation as hydroxides, followed by washing and dehydration. The dry catalysts were ground to pass a 100 mesh screen for incorporation with the coal and suspension medium in the preparation of the coal paste.

The equipment used, including the autoclave, has been described in detail (9). Automatic temperature control and a recording pressure gauge were used. The electrically heated autoclave was machined from 18:8 chrome nickel steel and supported in its furnace on a cradle permitting longitudinal rocking to ensure agitation of the contents. In this manner a troublesome packing gland necessary with a mechanical interior stirrer was eliminated and excellent continuous agitation obtained. An appropriate heated expansion valve, charcoal absorber, wet gas meter and water-sealed gas-holder completed the equipment.

Experimental Procedure

A standard procedure was used in all experiments except in regard to the analytical processes to be described.

The charge was prepared from weighed quantities of coal, medium and catalyst. All three were thoroughly mixed together and a weighed quantity of the resulting paste put in the autoclave after which closure was effected and a leak test carried out. Air was washed from the autoclave and tubing by means of hydrogen and the pressure of the hydrogen or other gas raised to the desired initial pressure, usually about 1000 lb. per sq. in. From the volume of the autoclave, paste and fittings, the amount of hydrogen could be calculated readily. The temperature was raised as rapidly as possible with the full power of the furnace to the operating temperature, between 400 and 500° C., and maintained constant for a chosen time. Agitation of the contents by rocking of the autoclave was begun when the temperature was about 100° C.; at this temperature the charge was quite fluid. At the end of the chosen reaction time, the heat was shut off and the autoclave cooled to room temperature or slightly above. Agitation was continued until the temperature was lower than 200° C. Agitation was very necessary at all temperatures where reaction or segregation of the coal was possible, in order to avoid the formation of a hard coke difficult of removal.

Considerable attention was necessary in regard to leaks as the temperature rose, and at the operating temperature. The copper gaskets appeared to yield at about 200° C. and the holding bolts required tightening before this occurred to avoid serious leaks. Again, when operating temperatures of 425° C. and upwards were used, frequent tightening of the holding bolts was necessary in most experiments to prevent the development of large leaks. The softness of copper and its ease of corrosion by sulphur compounds and erosion by liquids and gases at the operating temperatures used led to these difficulties. Another type of closure or the use of some other gasket material, although desirable, was not convenient. The magnitude of the leak was not determinable exactly but was not greater than 10% except rarely, and represented a loss of gases and liquids. It was generally less than the evaporation and mechanical losses incident to emptying the autoclave.

The gases in the autoclave were expanded to atmospheric pressure, passed through activated cocoanut charcoal absorbers, measured by a wet gas meter and stored in a gas holder. After the gas had stood for a time sufficient to reach uniform composition, a sample was withdrawn for analysis in an improved Bureau of Mines apparatus. The gain in weight of the absorbers represented gases and volatile liquids, of which about 30% consisted of butane or lighter constituents and 70%, pentanes and higher hydrocarbons.

The complete process has been termed a cycle. With the same charge of coal, catalyst and medium, the cycle was repeated by adding a fresh lot of hydrogen, and carrying out the heating, cooling and expanding from one to three times in different experiments. Finally, the autoclave was opened and

the oil, water and residue collected as rapidly as possible and kept in a stoppered container. Unavoidable losses of volatile material and some solid residue occurred at this point.

A variety of treatments were devised and examined for use on the material taken from the autoclave. The use of various solvents such as alcohol, ether, carbon disulphide and benzene permitted the separation of various fractions. Such methods were discarded in favor of a simple method producing three products, water, oils and solid residue.

The whole product, solid and liquid, from the autoclave was heated on an oil bath to 125° C. and the distillate condensed by means of an ice condenser. The distillate consisted of water and volatile oils. The water layer was acid and contained hydrogen sulphide in solution, and ammonia when ammonium molybdate was the catalyst. The residue was diluted with ethyl ether and filtered. The residue in the filter was washed with ether until free from soluble material. This solid residue varied in its composition from unchanged coal, in experiments where little action occurred, to a coke-like material that did not show appreciable decomposition on heating, in more successful experiments. It contained all the ash and catalyst. This residue was dried to constant weight and when corrected for the known ash and catalyst content represented unchanged coal. The ether solution of oils was distilled through a short fractionating column in order to recover the ether, the distillation being carried to 300° C. still head temperature. The residues in the flask, though differing widely in viscosity, were classified as pitch. Quantitative analysis was not carried out on the oil fractions. They were invariably unsaturated to some extent and aromatic in character. They distilled without decomposition only when tetralin was the medium and usually deposited red gums on standing.

Results and Discussion

The principal details of a sufficient number of experiments to illustrate the results are shown in tables, supplemented in three cases by graphs of pressure, temperature and time. The tables are largely self-explanatory. However, precise definitions of a few terms may be necessary. The time in hours per cycle represents the time that the autoclave was within 5° C. of the tabulated temperature. This does not represent the total hydrogenation time, as hydrogen absorption began at temperatures near 300° C. The pressures are averages of the values for all the cycles of a particular experiment. The initial and final pressures were measured at room temperature, the maximum pressures at the temperature tabulated. The absorption of hydrogen, yields of products, and loss are shown as percentage by weight of the total charge. The losses include evaporation, mechanical and leakage losses. The gas analyses are expressed in percentage by volume. Data on the yield of carbon monoxide and olefines have been omitted from the table though the amounts were determined in every case. They amounted to 0.1 to 1.5% each in various experiments. The conversion of coal represents the percentage by

weight of the original dry coal, including ash, that was converted to gases and liquids. The figure is based upon the recovered solid residue less catalyst which was the most accurately determined quantity. A degree of uncertainty attaches to this procedure since any coke formed by the medium would be included in this residue. The value may be considered a minimum value. The distillation data give the amounts of the various fractions, including water, boiling below the temperatures tabulated.

Hydrogenations with Complex Hydrocarbon Mixtures

Table II shows results obtained in three different types of experiment using respectively a distillation residue of hydrogenated bitumen, McMurray bitumen and a highly refined paraffin oil.

TABLE II
HYDROGENATION USING VARIOUS SUSPENSION MEDIA AND CATALYSTS

Medium and coal	Distillate from hydrogenated bitumen, Coal 424	McMurray bitumen, Coal 420	Liquid petrolatum, Coal 420
Experiment no.	94	95	96
Coal, gm.	450	450	450
Medium, gm.	550	450	450
Catalyst, 5%	—	AM	M
No. of cycles	1	1	2
Time, hr./cycle	3	3	3
Average temp., °C.	425	425	425
Average pressure, lb./sq. in.			
Initial	745	745	720
Maximum	3585	3240	3195
Final	930	890	745
Change per cycle	185	145	25
Gas yield, l./kg. of charge	59.8	61.4	127.3
H ₂ absorbed, %	0.1	0.2	0.4
Charge to liquids, %	—	14.5	13.3
Charge to solids, %	—	65.7	67.3
Charge to gas, %	3.4	3.0	5.6
Charcoal absorber, %	—	—	—
Loss, %	—	16.8	13.8
Gas analysis, %			
CO ₂	11.8	15.9	13.2
H ₂	33.8	31.1	34.8
C ₂ H ₆	22.2	18.7	22.3
CH ₄	23.2	16.9	16.4
Conversion of coal, %			
Liquids, % of charge			
Water	More solid residue was recovered than coal put in and liquid product was small in amount and not distilled.	0.6	2.3
Over at 175° C.		10.6	6.8
Over at 225° C.		20.2	2.3
Over at 300° C.		32.3	13.8
Pitch		24.4	8.5
Loss (dist.)		0	0
		47.1	20.7
			24.9
			38.2

NOTE:—AM = $(NH_4)_2MoO_4$; M = MoO₃.

Hydrogen absorbed, charge to liquids, charge to solids, charge to gas, charcoal absorber and loss are given as weight per cent of total initial charge.

Experiments 94, 95 and 96 with distillation residues do not constitute an absolutely fair test because the large amount of material reduces the quantity of hydrogen available for reaction. However, a study of the pressure changes

during the experiments showed little reaction, and subsequent examination of the autoclave contents confirmed this conclusion. Fig. 1 shows the pressure-time and pressure-temperature record of Experiment 96. The inflection in Curve B between 300 and 400° C. suggests some reaction, but the very high final pressures and absence of any large pressure drop at 425° C. with time shows such reaction to be slight. The final (cold) pressure was greater than the initial pressure. Virtually all the hydrogen admitted was recovered and considerable coking of the medium occurred. The solid residue weighed more than the original coal added and appeared to be largely unchanged coal mixed with some coke. The high paraffin content of the gases suggests extensive cracking of the medium. An experiment in which pure dry coal and hydrogen alone were used yielded somewhat similar results. No great change in the coal was apparent, no liquids or gases were formed and all the hydrogen was recovered.

Experiments 131 and 132, illustrating the use of McMurray bitumen as medium, were more favorable. Absorption of hydrogen, probably by the bitumen, began at 200 to 250° C., and the pressure fell thereafter until, at 425° C., it began to rise slowly. The total drop in pressure during this period of rising temperature was 500 lb. per sq. in. in Experiment 131. The second cycle showed reaction at 300° C., and the pressure began to fall steadily as soon as the constant operating temperature of 425° C. was reached. Experiment 132 at 450° C. was not so satisfactory. The pressure changes were not so favorable and extensive coking took place. It has been shown previously (9) that bitumen becomes highly unstable at temperatures much above 425° C. The coal conversion figure is uncertain and probably much too small.

Experiments 134 and 137 are comparable experiments in which liquid petrolatum was used as medium. The results are related in many respects to those obtained with bitumen. Reaction began at a higher temperature, 300° C. or more, as might be expected from the relative stability of the two media. The rate of hydrogen absorption was greater but the total pressure drop at reaction temperature was less in the case of Experiments 134 and 137. Considerable cracking became evident in Experiment 134 after the first hour at 450° C. Thereafter, the pressure rose rapidly and continuously. The

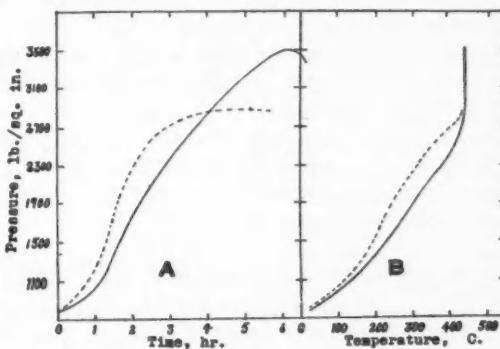


FIG. 1. Experiment 96. Pressure-time (A) and pressure-temperature (B) relations during hydrogenation at 450° C. with heavy oil as suspension medium. (—, Cycle 1; - - - , Cycle 2).

reduction in oil yield was large and the solid residue must have included much coke derived from the medium. The extent of reduction of coal to oils was as a consequence uncertain.

There would appear to be little difference in effectiveness as media between bitumen and liquid petrolatum at 425°. Coke and gas production was somewhat greater in the case of bitumen but such disadvantages could be controlled by choice of a more suitable catalyst and temperature. The use of liquid petrolatum has certain advantages in laboratory experiments, although its cost would be prohibitive for use on a large scale. The unstable nature of distillates from hydrogenated bitumen rule out their use entirely. It should be pointed out, however, that a stable heavy oil product could be obtained in the hydrogenation of bitumen.

Hydrogenation with Different Gases and Chemical Individuals as Media

The use of phenol as a medium in coal hydrogenation is common (13). Table III shows the results of four such experiments, and Fig. 2 is a graphic picture of the result of Experiment 101. This series showed that phenol

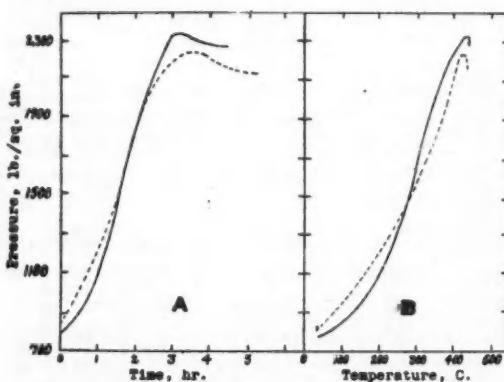


FIG. 2. Experiment 101. Pressure-time (A) and pressure-temperature (B) relations during hydrogenation at 425° C. with phenol as suspension medium. (----, Cycle 1; —, Cycle 2.)

that it is reduced to cyclohexane. Comparison of data of Table II with those on phenol shows that either bitumen or liquid petrolatum is definitely superior to phenol. With phenol, although the initial reaction temperature was about 350° C., the rate of reaction was much slower than in the other cases. The principal reason for not carrying on further experiments with phenol, however, was the difficulties in regard to treating the products.

The remaining four experiments (Table III) were carried out as an investigation of the properties of tetralin. This compound was first used as a suspension medium in the hope that it would be an ideal hydrogenating medium. The ease with which the compound may be dehydrogenated to naphthalene

is a satisfactory medium for hydrogenation of coal if, as in Experiment 102, an ample supply of hydrogen is used. It is unsatisfactory from the experimental point of view because of the difficulties attached to the treatment of the material recovered from the autoclave. This is contrary to the findings of Graham (13, 14) who has used phenol extensively with satisfactory results. The use of phenol has been condemned, however, by Lush (20) on the ground

or hydrogenated to decalin under the conditions of these experiments suggested that it would act on coal as a hydrogen carrier. In addition, its thermal stability and solvent power were favorable properties. A recent investigation by Hall (17) on the naphthalene-tetralin-decalin equilibria with hydrogen under conditions comparable to those of the present work has shown tetralin to be the principal individual product. Less than 10% each of naphthalene and decalin and about 40% of liquids boiling below 195° C. survive after five hours at 450° C. These results are in general agreement with the earlier researches of Spilker (27, 28) and Kling (19). Experiments whose results are given in Table III and subsequently in Tables IV and V show tetralin to be an excellent medium for the hydrogenation of coal. Experiment 129 was carried out on the assumption that naphthalene would serve as well as tetralin in that it would be hydrogenated to tetralin in the autoclave. It was believed that, with an ample supply of hydrogen, the

TABLE III
REDUCTION USING VARIOUS SUSPENSION MEDIA, CATALYSTS AND GASES

Medium	Phenol				Naphthalene	Tetralin		
	Hydrogen					Hydrogen	Natural gas	
Gas	98	99	101	102	129		Water gas	
Experiment no.	98	99	101	102	129	111	113	138
Coal no.	424	424	419	419	419	419	419	419
Coal, gm.	333	355	200	210	200	253	200	197
Medium, gm.	317	355	200	220	125	133	207	123
Catalyst, %	—	5%AM	5%AM	5%AM	4%M	2.5%M	5%M	5%M
No. of cycles	2	2	2	2	2	1	1	2
Time, hr./cycle	3	3.5	4	4	4	3	4	4
Average temperature, ° C.	425	425	425	425	480	450	450	450
Average pressure, lb./sq. in.								
Initial	720	745	790	810	1070	390	480	835
Maximum	2570	2740	2285	2290	2690	1730	1970	2495
Final	665	550	600	550	675	580	720	770
Change per cycle	-55	-95	-190	-260	-395	190	240	-65
Gas yield, l./kg. of charge	71.3	88.4	64.1	95.3	194	29.6	78.0	—
H ₂ absorbed, %	1.8	2.0	3.1	2.5	5.1	—	—	1.3
Charge to liquids, %	40.0	37.8	47.6	47.8	37.0	40.8	57.7	42.4
Charge to solids, %	45.4	48.0	41.7	36.6	35.3	43.5	24.3	35.8
Charge to gas, %	6.2	7.9	5.4	8.4	9.3	0.3	1.4	3.9
Charcoal absorber, %	—	—	—	—	1.5	0.8	1.7	3.6
Loss, %	8.4	6.3	5.3	7.2	16.9	14.6	14.9	14.3
Gas analysis, %								CO 14.6
CO ₂	15.3	14.8	5.6	5.7	3.1	7.9	5.6	14.2
H ₂	43.4	35.1	77.9	63.3	55.7	7.4	8.0	42.8
C ₂ H ₆	5.3	2.9	3.3	6.2	10.6	11.9	7.3	5.2
CH ₄	21.5	34.4	10.3	16.1	21.7	62.6	65.2	15.8
Conversion of coal, %	11.4	4.7	22.5	30.9	47.5	35.5	68.0	46.7
Liquids, % charge								
Water								0.4
Over at 175° C.								3.5
Over at 225° C.								29.7
Over at 300° C.								34.8
Pitch								7.6
These liquids were separated by fractional solution and were not distilled. They contained much phenol.								

NOTE:—AM = $(NH_4)_2MoO_4$; M = MoO₃.

same hydrogenation equilibrium would be set up with naphthalene as with tetralin. The result was as expected. A high hydrogen absorption and coal conversion resulted. Only a part of the naphthalene added was recovered in the products of the reactions, together with considerable tetralin. The high maximum pressure was probably due to the greater volatility of naphthalene and tetralin compared to that of other solvents used.

Experiments 111 and 113 were carried out with a view to demonstrating that tetralin was capable of hydrogenating coal in the absence of hydrogen, with the production of naphthalene. The small production of hydrogen suggests a direct transfer of hydrogen from tetralin to coal. The oil contained a great deal of naphthalene and relatively little tetralin. The increase in yield of liquids and conversion of coal resulting from an increase in the proportion of tetralin in Experiment 113 confirms the suggested mechanism of the process. Part of the increase in yield may be due to doubling the amount of catalyst. The oils produced in these experiments appeared to be of a higher quality and thermally more stable than those produced with other media. Experiments 129, 111 and 113 pointed to the conclusion that tetralin was an excellent medium and acted on the coal essentially as a hydrogen carrier as well as a solvent.

The last experiment in Table III, No. 138, was carried out with a definite aim in view, the conservation of hydrogen. The relatively large amount of oxygen in Alberta coals, apart from that held as water, requires considerable hydrogen for its reduction to water. Such water may be considered as waste from the point of view of oil production. Water gas is considerably less costly than hydrogen, and is a reducing gas that should act as effectively as hydrogen on the oxygen of coal. The results obtained in Experiment 138 showed that water gas, with a tetralin medium, was an effective reducing gas. Further, the oxidation of the carbon monoxide by oxygen in the coal occurred to a considerable extent, the ratio of hydrogen to carbon monoxide in the gas rising from 2.0 before to 2.93 after the experiment. The gas produced in both cycles of the experiment had much the same composition. The large production of carbon dioxide and greatly reduced production of water lead to the conclusion that carbon monoxide will remove oxygen from the coal as readily as will hydrogen. Finally, the comparatively good conversion in this experiment with a small hydrogen absorption points to the conclusion that, in other experiments, much of the hydrogen absorbed is used up in the formation of water. This experiment suggests that considerable economies would be effected with a procedure using water gas in one or two cycles, and hydrogen for a final treatment.

Hydrogenations with Tetralin as Medium

The use of tetralin as suspension medium for coal was investigated with the two coals, Nos. 419 and 420. Several of the results are given in Tables IV and V. Some conclusions can be drawn from a consideration of the experiments as a whole.

An immediately noticeable result was the nature of the material in the autoclave after an experiment. The coal, ash and catalyst residue were not in the form of a coke but remained in suspension in the liquids. The oils were thermally stable. The conversion of coal to liquids and gases was high, 91% in one case and frequently more than 80%, although the coals contained 9-10% ash. The gas pressures were never excessively high even at 470° C. Reference to Table IV shows a rough parallelism between the production of water and the number of cycles. This in conjunction with the result, not tabulated, that most of the carbon dioxide produced was liberated in the first cycle, suggests that there are two types of oxygen in the coal. It is probable that much oxygen is combined in carboxyl groups and is liberated by thermal decomposition as carbon dioxide, and that the remainder of the oxygen is combined as hydroxyl groups and removed much less readily by hydrogenation to water. In this connection the results of Experiment 138, Table III, should be considered, as a question arises as to which type of oxygen is reduced by carbon monoxide. It is believed that the increase in carbon dioxide production in this experiment results from reduction of hydroxyl by carbon monoxide. Parr and Hadley (21) have found that carbon dioxide is liberated by thermal treatment of coal. Tropsch (29) believes that the water produced by hydrogenation of coal originates in phenolic bodies.

TABLE IV
HYDROGENATION OF COAL 419 WITH TETRALIN AS MEDIUM AND WITH VARIOUS CATALYSTS

Experiment no.	103	110	112	136	139	140	141
Coal, gm.	200	240	252	200	197	196	213
Tetralin, gm.	200	120	127	150	123	124	131
Catalyst, %	5%AM	5%M	5%M	5%MC	5%FC	5%MC	5%FC
No. of cycles	2	2	4	2	2	1	2
Time, hr./cycle	3.5	4	4	4	4	4	4
Average temperature, ° C.	450	450	450	470	450	425	450
Average pressure, lb./sq. in.							
Initial	965	965	1075	1010	975	1055	945
Maximum	2335	2500	2665	2690	2595	2330	2640
Final	470	585	665	635	585	580	625
Change per cycle	-495	-380	-410	-375	-390	-475	-320
Gas yield, l./kg. of charge	82	146	315	136	98	50	107
H ₂ absorbed, %	4.1	3.3	6.1	4.3	3.9	2.4	3.4
Charge to liquids, %	72.5	58.1	55.0	60.0	70.0	64.7	55.5
Charge to solids, %	14.3	21.6	15.8	19.5	13.4	22.5	23.6
Charge to gas, %	3.0	7.6	6.3	9.4	5.6	4.8	9.1
Charcoal absorber, %	—	—	1.0	3.3	3.4	1.8	3.0
Loss, %	10.2	12.7	21.9	7.8	7.6	6.2	8.8
Gas analysis, %							
CO ₂	3.9	5.1	2.4	2.8	4.3	6.8	4.3
H ₂	70.0	58.9	74.2	64.5	74.5	70.4	70.4
C ₂ H ₆	2.8	12.2	5.8	14.6	4.7	4.7	4.1
CH ₄	16.1	16.0	9.7	11.3	12.6	13.5	18.4
Conversion of coal, %	80.0	74.2	83.0	72.0	83.5	70	67.7
Liquids, % of charge							
Water	6.7	11.2	7.1	—	1.8	4.9	
Over at 175° C.	18.5	22.4	21.0	6.8	4.3	10.8	
Over at 225° C.	28.4	43.5	46.4	38.1	39.7	39.6	
Over at 300° C.	48.0	47.0	50.8	47.9	46.8	45.5	
Pitch	10.1	8.0	9.2	22.1	17.9	10.0	

NOTE:—AM = $(NH_4)_2MoO_4$; M = MoO_3 ; MC = $MoO_3 \cdot Cr_2O_3$; FC = $Fe_2O_3 \cdot Cr_2O_3$.

TABLE V
HYDROGENATION OF COAL 420 WITH TETRALIN AS MEDIUM AND WITH VARIOUS CATALYSTS

Experiment no.	119	120	121	135	124	125	126	127
Coal, gm.	200	205	200	200	200	200	200	200
Tetralin, gm.	109	105	100	165	105	110	135	125
Catalyst, %	5% M	5% M	5% F	6% FC	5% F	5% F	4% FC	7% FC
No. of cycles	1	4	2	2	4	2	2	2
Time, hr./cycle	1	4	3	4	4	4	4	3
Average temperature, °C.	450	450	450	450	470	470	470	470
Average pressure, lb./sq. in.								
Initial	1235	1190	1120	955	1000	990	1030	1060
Maximum	2625	2820	2455	2385	2510	2405	2290	2570
Final	670	875	765	570	680	625	—	610
Change per cycle	-565	-315	-355	-385	-320	-365	—	-450
Gas yield, l./kg. of charge	52	217	123	96	254	140	133	133
H ₂ absorbed, %	2.8	5.6	3.3	3.5	5.9	3.6	4.5	4.1
Charge to liquids, %	66.6	59.4	56.8	75.5	32.8	48.7	40.3	55.4
Charge to solids, %	21.6	16.8	22.8	9.9	30.5	22.6	21.8	18.5
Charge to gas, %	1.7	7.5	5.0	8.3	12.9	7.0	6.6	8.1
Charcoal absorber, %	2.3	1.8	1.0	0.6	1.3	0.5	0.0	0.8
Loss, %	7.8	14.5	14.4	5.9	22.5	21.2	31.3	17.2
Gas analysis, %								
CO ₂	0.4	0.3	1.1	0.7	0.4	0.5	1.0	0.9
H ₂	76.4	80.2	75.8	70.8	74.0	67.3	65.0	68.5
C ₂ H ₆	3.0	4.0	5.5	10.5	6.0	8.5	7.2	10.9
CH ₄	11.6	6.8	9.6	14.1	12.8	13.3	19.0	12.7
Conversion of coal, %	72.5	80.4	71.5	91.0	58.5	71.0	68.2	78.0
Liquids, % of charge								
Over at 175° C.	10.0	13.1	3.4	13.7	11.2	8.4	9.0	9.5
Over at 225° C.	42.9	42.9	33.4	43.1	25.0	34.1	31.0	32.2
Over at 300° C.	57.3	50.8	39.4	47.8	28.4	37.6	34.4	43.4
Pitch	9.3	8.6	17.4	27.7	4.4	11.1	5.9	12.0

NOTE:—M = MoO_3 ; F = Fe_2O_3 ; FC = $Fe_2O_3 \cdot Cr_2O_3$.

A comparison of the data of Tables IV and V from the point of view of the type of coal used does not allow of any certain conclusion being drawn. On the whole, Coal 419 appeared to be more susceptible to hydrogenation, as might be suspected from its classification as sub-bituminous. On the other hand the bituminous coal, No. 420, gave greater yields of oil and less water, and showed the maximum conversion of 91% in Experiment 135 with an iron-chromium catalyst. The effect of a temperature greater than 450° C. was generally adverse, as shown by increased gas yield and increased solid residue. Hall (17) has shown in work on the hydrogenation of naphthalene to tetralin that marked decomposition with the formation of gas and coke occurs at 460° C. or higher. No great increase in coal conversion was obtained by using more than two cycles. Usually a small increase was observed but at the same time the yield of liquid decreased and the gas production increased.

A study of the reaction by following the pressure-time-temperature curves showed some interesting results. Fig. 3 gives the record for one experiment, No. 110, and may be taken as typical. Hydrogen absorption began at about 300° C. with a rising temperature. Distinct evidence of an exothermic reaction was always obtained in these hydrogenation experiments when hydrogen absorption began. The rate of temperature rise showed a sudden

increase in the neighborhood of 300° C. Usually the pressure began to drop before the temperature reached 400° C., and for the first half hour at 450° C. fell with great rapidity. After one to one and one-half hours at 450° C. the pressure became constant. It is believed that hydrogen absorption continues, however, and is balanced more or less by gas production. The second cycle of the experiments showed generally similar results, which were modified as expected by a higher maximum pressure and smaller rate of pressure drop. The relative amounts of coal and tetralin had a definite influence on the pressure developed and on the coal conversion. Increased amounts of tetralin resulted in an increased conversion and decreased maximum pressure. The influence was slight but indicated that at least three parts of tetralin to four of coal should be used for satisfactory operation.

An estimate of the relative value of the various catalytic mixtures is difficult to make from the tabulated data alone and requires consideration of the pressure-time relations. A catalyst may have two important effects; it may promote hydrogenation and it may promote thermal decomposition. Undoubtedly both reactions occur under the experimental conditions and are promoted to some extent by a catalyst. In addition the quantity and quality of the oils produced and the quantity of gas produced depend upon the effect of the catalyst on the two reactions. From the point of view of maximum conversion of coal to liquids, the equimolar mixture of iron and chromium oxides was the best catalyst. Of the others, only molybdc oxide need be considered. This caused smaller total conversion than did the iron-chromium mixture, but had the advantages of producing a superior oil from the point of view of unsaturation and pitch content, and of resulting in a higher rate of hydrogen absorption. Though the iron-chromium mixture promoted liquefaction of the coal it promoted also thermal decomposition to a greater extent than did molybdc oxide. For a systematic investigation, not yet reported, of a number of Alberta coals, molybdc oxide was chosen as the best catalyst.

A few observations regarding the liquid products are of interest. The water obtained on distillation was invariably acid. The acid constituents were not identified except by demonstrating their organic nature and volatility. The oils were different in many respects from those produced with other media. Fractional distillation of the 175 – 225° C. fraction showed the presence

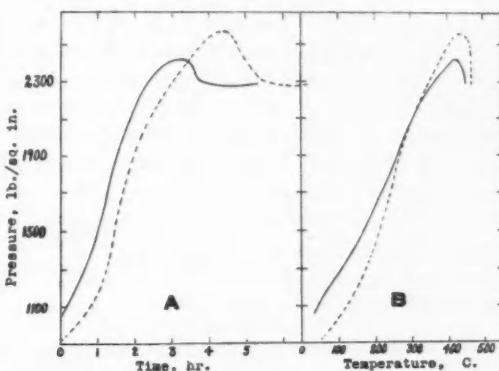


FIG. 3. Experiment 110. Pressure-time (A) and pressure-temperature (B) relations during hydrogenation at 450° C. with tetralin. (—, Cycle 1; - - -, Cycle 2.)

of a large amount of material boiling between 195 and 215° C., presumably tetralin, naphthalene and decalin, for the most part. The remainder of the oil fraction was chiefly notable by its stability when distilled at atmospheric pressure to 450° C. No decomposition occurred. From 225 to 350° C. the distillate was a heavy yellow fluid of apparently high viscosity. Occasionally, colorless, wax-like crystals separated from this distillate during the later stages of the distillation. At about 350° C. the color of the distillate changed to red and the distillate from the final stages of the distillation became solid or semisolid at room temperature. At 450° C., about 5% of the original coal remained as pitch, which boiled quietly at 450° C. and on cooling solidified at about 200° C.

Summary and Conclusions

These experiments show that the Alberta coals examined are readily hydrogenated to an extent depending largely upon the medium used. A suspension medium is necessary in order to obtain a reasonable rate and yield in the process and the results emphasize the importance of a suitable choice. A heavy residual oil, such as may be obtained from hydrogenated bitumen, was unsatisfactory because of its instability and probable lack of solvent power. Bitumen showed some promise as a medium and was reduced itself, probably more than the coal. Liquid petrolatum appeared to be a fairly effective medium for laboratory purposes, but had the disadvantage of suffering considerable decomposition to coke in the process. Phenol was of some value, chiefly because of its stability, but it had the great disadvantage of precluding a simple procedure for the analysis of the products. Tetralin was much superior to the other media in promoting rapid and extensive liquefaction of the coal.

Roughly speaking, the effectiveness of a medium paralleled its ease of hydrogenation and dehydrogenation. The results suggested that tetralin acted both as a good solvent and as a hydrogen carrier, the latter function overshadowing the solvent action and the effect of any added catalyst. The suggested mechanism is one of transfer of hydrogen from tetralin to the coal compounds and the hydrogenation of the resulting naphthalene to tetralin again by hydrogen. The experiments with tetralin and natural gas and with naphthalene and hydrogen, together with the presence of naphthalene in the oils of Tables IV and V, confirm the hydrogen carrying action. It has been shown elsewhere that tetralin is readily prepared from naphthalene by hydrogenation and is just as readily dehydrogenated (12), and that tetralin is a good hydrogenating agent in the presence of palladium (1). There is an obvious field for further work in the examination of other compounds capable of reversible hydrogenation and stable under the conditions of these experiments.

The maintenance of high hydrogen concentration in the autoclave and effective temperature control between 425 and 450° C. were shown to be optimum operating conditions.

The oxygen content of the coal appeared mostly as carbon dioxide and water. It was suggested that the carbon dioxide arose from decomposition of carboxyl groups and the water from hydrogenation of hydroxyl groups. An experiment in which a mixture of hydrogen and carbon monoxide was used in place of hydrogen showed an apparent reduction of phenolic compounds by carbon monoxide.

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REVIEWS AND NOTES

SENSITIVITY AND OUTPUT OF VARIOUS TYPES
OF PHOTOCELLS¹By R. RUEDY²

Abstract

When the current sensitivity of a short-circuited photo-emissive cell is defined in the same manner as the grid-plate conductance of a vacuum tube, the ratio microamperes to lumens in modern photo-tubes is of the same order as the ratio milliamperes to volts in vacuum tubes, but a change of one lumen corresponds to virtually the entire range, 1 ft.-candle to 1000 ft.-candles, concerned in problems of illumination. Taking into account the detector action and the retarding voltage across the load used with a barrier film cell, the resistance giving the highest output of power is nearly equal to $(\frac{1}{2} kIG)^{\frac{1}{2}}$, provided that I be less than 1000 ft.-candles and that the film rectifies according to a square law, Gv^2 . It is advisable to develop cells possessing relatively small values of G and an exponent of ν not larger than two.

In industrial work, photoelectric cells are often used with an appreciable load in the circuit, consisting, in the simplest case, of a high resistance or of a coil which forms part of a relay or a transformer (1, 4, 6). It has been rightly said that no photocell is better than the circuit in which it is used; on the other hand, though the sensitivity of the best photo-emissive, barrier film or photoconducting cells may be of a similar order, their internal resistance depends on the illumination in a manner which differs considerably from one type to another. Moreover, in the case of the more recent barrier film cell, the load inevitably is in parallel with the internal resistance; in the other cells it is in series with the internal resistance. If a device is to be actuated by a photocell, the question arises—which type of cell accomplishes the task most efficiently? As an illustration, the response of different cells having about the same sensitive area, 1 sq. in. (6.45 sq. cm.), may be compared when they are exposed to an illumination, I , of 10 ft.-candles, the intensity sometimes recommended for offices, factories and showrooms, and also when this value increases or decreases by 10%. The smallest variation which the eye can detect when comparing two fields side by side is about 1%.

For a sensitive surface of 1 sq. in. the mean light flux at 10 ft.-candles is about 0.07 lumen (or between $1/14$ and $1/15$ lumen). The load may be either a coil of 50,000 turns and a resistance, R , of 10,000 ohms, with a contact which, in order to be brought from the open to the closed position,

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requires a change of about one milliampere in the current flowing through the coil (telephone relay); or the load may be an ohmic resistance of about 10 megohms, placed across the grid of a vacuum tube.

For a good photo-emissive vacuum cell (caesium oxide cell) the current, i , is a function of the applied voltage, E , divided by the sum, $R + r$, of the external and the internal resistance, the voltage drop produced across the load being equal to Ri . Provided that the cell always operates above saturation, the resistance, r , which it offers to small changes, the so-called a-c. or internal resistance, is much higher than that of any current-carrying device likely to be connected to the cell, and the current is independent of the applied voltage so that $i = gl$, where g , the current sensitivity, is constant and independent of l . The change in current, or in voltage, is proportional to the change in foot-candles or lumens, whatever the initial intensity of the light. In the best cells, giving about 50 μ a. per lumen when exposed to the light from a tungsten filament at 2700° K., the current changes from about 3.5 μ a at 10 ft.-candles to 3.2 or 3.9 μ a. for a 10% increase or decrease in the illumination, and the power in a 10,000 ohm coil, used as a relay, varies by only a small fraction of a microwatt, an amount far too small to operate a sensitive relay. On the other hand, with an internal resistance of over 1000 megohms, the cell readily causes a drop of 3.5 volts across a 10 megohm resistor, a change which suffices for controlling the grid of a three-electrode tube over the linear range. The voltage change in the 10 megohm load amounts to 500 volts per lumen.

The current sensitivity, g , of a vacuum photocell is sometimes likened to the mutual conductance, G_m , or grid-plate conductance, of a radio tube, changes in illumination playing the part of changes in the grid voltage. On this basis the amplification factor, μ , of the radio tube corresponds to the change in plate voltage necessary for producing a small variation in the current, divided by the change in illumination which would cause the same variation in current in the absence of any external load. For those vacuum cells in which the sensitive surface is a solid piece of metal, in contrast to the modern cells with composite films—the silver-oxygen-caesium cell, for instance—the value of this factor lies beyond any definite limit, because the saturation current is clearly defined, and above saturation no change in anode voltage, however great, alters the current. When however the change in voltage across the load is considered, the output voltage sensitivity per lumen becomes equal to gR , an expression which corresponds to the voltage amplification, G , in a complete vacuum tube circuit. G , indeed, is equal to $\mu R/(R + r)$, or to $G_m R$ when the internal resistance r is very high (3).

In the *gas-filled photoelectric tube* the internal resistance decreases after the saturation stage has been passed, and ionization of the gas by the electrons, increasing according to an exponential law, has become appreciable. The current sensitivity may be raised to 5 or 10 times the value obtained in vacuum before the operation of the cell tends to become unstable and a given reading difficult to reproduce. In the tubes used in practice the change in current,

in microamperes, produced by a change in illumination of one lumen is of the same order as the change in milliamperes produced in a three-electrode tube when the grid bias varies by one volt. A change of one lumen corresponds to the difference between 1 ft.-candle and 1000 ft.-candles (the light intensity in the shade outdoors on a bright day), the entire range concerned in problems of illumination. The voltage sensitivity, μ , or amplification factor, of the cell assumes a finite value which varies, however, from one intensity, l , to another, since $g = \mu/r$ and r varies with the illumination. The output voltage sensitivity may be expressed as $\mu R/(R + r)$, where the magnitude of r now may drop to nearly that of R .

In the *barrier film cell* (cuprous-oxide-copper cell, selenium film cells, including the Photronic cell as a special case), the current obtained is strong, but an appreciable number of electrons, which the light has set free and forced through the barrier plane into the electrode, return immediately to their place of origin, forming a local short-circuit current, b , which is in parallel with the photoelectric current, i , flowing through the load, R . As long as the voltage drop in the load is quite small, or the load negligible, the relation between current, i , and illumination is given by the expression for a parallel circuit

$$i = i_0 \frac{r}{R + r} = \frac{kr}{R + r} l ,$$

where r is the internal resistance which the cell offers to the local short-circuit current. No external voltage is applied to barrier film cells; the metal which is in contact with the non-conducting film becomes the negative electrode (1, 6, 8). A comparison with the radio tube is no longer useful.

When the variation, dr/dl , in the resistance of the barrier plane, is negligible compared to r

$$\frac{di}{dl} = \frac{kr}{R + r} ,$$

and the output voltage sensitivity is R times this value, or when R is very large, equal to kr . The load, R , for which the power output reaches its highest value is found by studying the changes in i^2R with l ; it is equal to r , whatever the value of l , and changes in power caused by changes in illumination are also largest at this value, namely equal to $k^2rl/2$.

For a rear-wall cuprous oxide cell, 1.5 in. in diameter, r may be made equal to 100 ohms, and k is equal to 100×10^{-6} amp. per lumen (7). The output voltage sensitivity thus is only 1/100 volt per lumen for $R = 10$ megohms. On the other hand, when the coil is used, a change of 10% in the illumination, assumed to be 10 ft.-candles, changes the photo-current by nearly 0.5 μ a. The change obtained, without any external voltage applied to the cell, can be read on a portable instrument. The highest power sensitivity, $k^2rl/2$ watt per lumen when $r = R$, reaches $\frac{1}{2}$ microwatt per lumen. The maximum power output amounts to $k^2l^2r/4$ watts. Supersensitive relays of 300 ohms resistance require about 250 μ a. for their operation; they are

capable of establishing contact for currents less than 0.2 amp. at six volts. One of the most sensitive relays of the galvanometer type works with $2\mu\text{a}$. or 0.5 mv. and handles five watts at 40 volts with ohmic load.

In the general case, particularly in the selenium film cells, the total current, the sum of i and b , is not really proportional to the light received by the sensitive surface, owing to the voltage drop produced across the load, which tends to prevent all but the fastest electrons from crossing the barrier film. The load thus produces the same effect as an opposing potential applied to a cell carrying no load (5). In this case a certain voltage, V_0 , is capable of suppressing the photoelectric current altogether. The voltage, V_0 , depends on the highest velocities which the electrons possess after they are set free; it is of the same order, in practice, as the open-circuit voltage, namely a few tenths of a volt. The shorter the wave-length of the light that falls upon the cell, the higher is V_0 . Moreover, the barrier film behaves as a rectifier rather than as a parallel resistance, r , to which the resulting potential drop is applied. For the Photronic cell the effect becomes appreciable when v exceeds 40 mv. (8). The resistance of the selenium film, finally, is so high that it must be taken into account by a resistance (ρ) placed in series with the external resistance, R (Fig. 1).

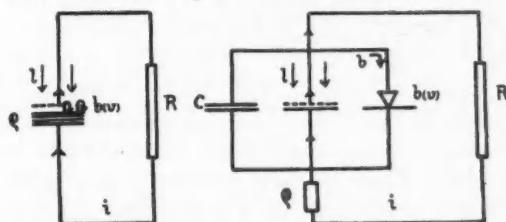


FIG. 1. Actual circuit (left) and equivalent circuit (right) of a barrier-plane front-wall cell.

If the decrease, caused by the counter e.m.f., in the number of electrons which succeed in traversing the barrier plane is assumed to conform to a straight line law from i_0 , the value obtained at short circuit and equal to kl , down to zero when the circuit is open and the voltage v equal to V_∞ , then

$$i = i_0 \left(1 - \frac{v}{V_\infty} \right) = \frac{v}{R + \rho} + b(v),$$

where $b(v)$ is governed by the rectifying properties of the barrier film. The voltage v corresponding to a given l may be determined from this equation, provided that the rectifying properties of the cell and the behavior of the short-circuited illuminated cell relative to a retarding potential applied to it have previously been established, and are available in the form of graphs or formulas. The current is R times smaller. In any case

$$v = \frac{\frac{i_0}{i} - \frac{b(v)}{i_0}}{\frac{1}{V_\infty} - \frac{1}{R + \rho}}.$$

For an ideal rectifier $b(v)$ is a function Gv^x for positive values of v , and virtually zero, or equal to a small value, gv^y , for negative values of v . In the simplest case and for large changes in l , the exponent x is equal to unity, so that

$$v = \frac{kl}{\frac{kl}{V_\infty} + \frac{1}{R + \rho} + G}.$$

Hence the voltage produced is no longer proportional to the illumination. The ohmic load, R_h , giving the highest output of power,

$$R_h = \rho + \frac{1}{\frac{kl}{V_0} + G} ,$$

is nevertheless independent of l , since kl/V_0 is small. For very small values of $(R + \rho)$, the current $i = v/(R + \rho)$ may be expressed as follows:

$$i = kl(1 - G(R + \rho)) - kR \frac{R + \rho}{RV_0} R^2 = kl - K R^2 .$$

Empirical formulas of this type agree with the measured values, R^2 being replaced if necessary by l^2 .

For the general type of barrier film cell, $b(v)$ is more accurately given by Gv^2 , where G is about 1/20 for the cuprous oxide, and 1/160 for the selenium barrier cell. The voltage becomes

$$v = \frac{-\left(\frac{kl}{V_0} + \frac{1}{R + \rho}\right) + \sqrt{\left(\frac{kl}{V_0} + \frac{1}{R + \rho}\right)^2 + 4klG}}{2G} .$$

The resistance, ρ , which the electrons coming from the outside circuit must overcome before they can complete their journey back to the barrier film, is of the order of 30 to 100 ohms in the case of selenium, and smaller for cuprous oxide cells (selenium having a specific resistance of $\frac{1}{4}$ to $\frac{1}{2}$ megohm, cuprous oxide 600 to 100,000 ohm per cc. depending on traces of cupric oxide present).

When the last term under the root sign is much smaller than the square, and R larger than ρ , the current becomes equal to

$$i = kl - \frac{R + \rho}{RV_0} R^2 = kl - K R^2 ,$$

as before. A similar formula in which R^2 is replaced by $l^{1.75}$ is valid between 25 and 250 ft.-candles for the Photronic type of selenium cell, as long as the load used at the stronger intensity does not exceed 700 ohms.

By computing $v^2 R / (R + \rho)^2$ and differentiating with respect to R , the resistance, R , giving maximum power output for a given illumination, is obtained by solving the equation.

$$\left(\frac{kl}{V_0} + \frac{1}{R + \rho}\right)^2 + 4klG - \frac{R^2}{(R^2 - \rho^2)^2} = 0 ,$$

or

$$R^4 \left(4V_0G + \frac{kl}{V_0}\right) + 2R^3 - R^2 \left(2\rho + \frac{3V_0}{kl} + 2\rho^2 \left(4V_0G + \frac{kl}{V_0}\right)\right) - 2R\rho \left(\rho + \frac{V_0}{kl}\right) + \rho^2 \left(2\rho + \frac{V_0}{kl} + \rho^2 \left(4V_0G + \frac{kl}{V_0}\right)\right) = 0 .$$

On introducing the values k and V_0 valid for selenium film cells ($k = 2 \times 10^{-8}$ amp. per metre-candle or lux, $V_0 = 0.6$ volt) this expression reduces to

$$R_h = \sqrt{\frac{3}{4klG}}$$

for the entire range of illumination from the lowest values nearly up to the intensity outdoors in sunlight, about 100,000 metre-candles. When l is made 10 times larger, R must be made 3.17 times smaller, according to this formula, in order to secure the highest power. In practice an even greater reduction, between 5 and 7, is found necessary to obtain this result, indicating that the exponent x in the law Gv^x is probably larger than two. The empirical formula just mentioned gives

$$R_h = 0.24V_0/sl^x ,$$

which corresponds to a ratio of 5.6 for the resistances R_h , when l is increased 10 times its value.

Though the selenium barrier cells have recently been improved so as to give more nearly reproducible readings while losing very little of their sensitivity, an important factor in meteorological work, the necessity of decreasing the resistance in order to obtain a high power output at high intensities is still a serious drawback when the direct conversion of light into electrical power is considered. The theory would indicate that in this respect the development work should aim at producing barrier films which rectify according to a law involving no higher powers of the voltage than the second.

At values of l below about 100 ft.-candles (1 ft.-candle = 10.76 metre-candles or lux), the values of R_h are quite large, and as the open circuit voltage, for $R = \infty$, is given by the expression $V_\infty = \sqrt{kl/G}$, and the short circuit current i_0 is equal to kl , the highest power output for a given illumination may be written as

$$L_h = 1.15 i_0 V_\infty .$$

Taking the constants of a typical selenium-iron cell, 14 mm. in diameter, k between 10^{-8} and 2×10^{-8} amp. per metre-candle, $G = 1/160$, L_h has a value between 0.4 and 1.1 μ w. at 1000 metre-candles against the measured value of 0.7 μ w. (5). Reducing l to one-tenth or about 10 ft.-candles brings L_h down to 1/32 of its former value. The current obtained, however, is still appreciable, about 60 μ a., so that a 10% change could be readily detected. The low output is due to the low voltage produced, only about 20 mv., whereas the normal vacuum photoelectric cell, in the absence of any external potential, would produce about 700 mv. between closely spaced electrodes, regardless of the illumination. But in this case the output is small, owing to the very high internal resistance.

Finally the change in the resistance, $1/G$, of the photoconductive cells, which respond to the light almost like gas-filled photo-emissive cells, is proportional to the n th power of the illumination:

$$G = G + kl^n = 1/r = \frac{1 + kl^n r_0}{r_0} .$$

For selenium the value of n lies between one-quarter and one-half. The resistances in the dark range from one-half to several hundred megohms, depending upon the heat treatment which the selenium has undergone. The object of the treatment is to make G equal to at least $2G_0$ when l is about

10 ft.-candles. In the most sensitive cells G may be as high as $50 G_0$ under the same conditions, so that the conductance in the dark may be neglected. From $i = E/(R + r)$ it follows that

$$\frac{di}{dl} = \frac{di}{dr} \frac{dr}{dl} = \frac{nkEl^{n-1}}{(R + r)^2 (G_0 + kl^{n-1})^2},$$

or when the load R is made equal to $r/2$ to ensure highest sensitivity

$$\frac{d(i^2 R)}{dl} = \frac{d(i^2 R)}{dr} \frac{dr}{dl} = \frac{2nkE^2 R r^2 l^{n-1}}{(R + r)^3} = \frac{8nkE^2 l^{n-1}}{27}.$$

Even when n is not less than $1/2$, the sensitivity is very high in the lower range of illumination, and under these conditions, the photoconductive cell still remains virtually the only cell capable of directly operating ordinary telephone relays. The change in potential across high resistance cells also suffices for the control of electronic or ionic tubes.

In view of the many endeavors to improve the available photoelectric cells it is of interest to examine the maximum mechanical work which they may be expected to yield in the absence of an external electromotive force. During the brightest hours of the day, each square centimetre, when placed normally to the sun's rays, receives about 0.12 watt per sec. Of this energy, one-third lies in the visible, and another third between the visible and the wave-length 1.2μ ; one-tenth is in the ultra-violet. The cell is not sensitive to radiation of wave-length greater than 1.2μ . Even assuming complete absorption and transformation into mechanical energy, the incident energy could not actuate ordinary telephone relays without being amplified. Supposing that in the visible the average quantum amounts to 3.3×10^{-12} erg, whereas in reality it varies from 5×10^{-12} in the blue to 2.6×10^{-12} at 0.76μ , and that one quantum sets one electron free, one watt of sunlight would produce a current of five amperes, so that neglecting space charges, the potential produced by the cell would be at the most 0.2 volt. With artificial sources of light, an incandescent body at 2710° K., for instance, the same degree of illumination as produced by the sun, 100,000 metre-candles, corresponds, of course, to a much larger amount of radiant energy, because the greater part of the visible radiation lies in a region to which the eye is several times less sensitive than to sunlight, and because the proportion of energy radiated between the visible and 1.2μ is nearly one-third, in contrast to $1/12$ in the visible. The output of photocells ought hence to be referred to the total incident energy.

Despite the capacities associated with the cells, the computed sensitivities, perhaps with the exception of those of the ordinary selenium resistance cell, are also valid for rapidly repeated changes in the intensity of illumination, provided that the frequency does not exceed 500 or 600 cycles per second. It is therefore possible to illustrate and study one of the main differences among the various cells, the great voltage sensitivity of the photo-emissive type and the great current sensitivity of the selenium barrier film cells, by using a telephone receiver as a load and exposing the cell to the light from

lamps operated on 60 cycles. Barrier film cells render the 120-cycle fluctuation in the light of the lamps, amounting to a few per cent, definitely audible: photo-emissive tubes require one stage of vacuum tube amplification; the same amplification would be useless when applied to barrier film cells.

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